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Top-down control of visual attention and awareness: Cognitive and neural mechanisms

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Abstract

Recent behavioural and neural research suggests that awareness is intimately related to top-down cognitive functions such as attention. Here I present a characterization of this relationship, guided by Lavie's load theory. Load theory proposes that perception has limited capacity but proceeds automatically on all stimuli (whether relevant to the task at hand or not) until capacity is exhausted, and that the allocation of processing resources to certain stimuli (rather than to other, competing ones) is guided by executive control functions such as working memory. The theory predicts that increasing the perceptual load of a task will consume capacity, therefore reducing processing of stimuli external to that task; it also predicts that increasing working memory load will impair executive control, leading to increased processing of salient ignored stimuli. Here I show that these predictions hold not only for indirect measures of perceptual processing, as has been demonstrated previously, but also for visual awareness – the subjective experience of seeing and being able to report the nature of a visual stimulus. I find that under high perceptual load, observers become less aware of the very presence of other stimuli, even when these stimuli are fully expected and serve as targets. I also show that perceptual load affects the temporal resolution of visual awareness – under high load, the ability to detect a temporal pattern (luminance flicker) is reduced, leading to a subjective percept of steady illumination. In a neuroimaging study, I show that subjective awareness of flicker is associated with activity in frontal and parietal brain regions previously associated with attention and awareness. Next, I investigate the role of executive control in visual awareness by examining the effect of working memory load on

binocular rivalry, a fundamental form of visual competition. I find that high working memory load reduces dominance durations in rivalry, suggesting that working memory may serve to maintain perceptual biases during competitive interactions in visual awareness. Finally, I use Transcranial Magnetic Stimulation to establish a causal role for the previously described right parietal involvement in the control of binocular rivalry. This research therefore indicates that top-down cognitive and neural mechanisms are involved in determining whether visual stimuli will reach awareness, and in shaping the subjective nature of the experience such stimuli evoke.

I, David Podhorzer Carmel, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

The study presented in Chapter 4 of this thesis has been published with my supervisors, Nilli Lavie and Geraint Rees, as co-authors. The full citation for the published paper is:

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Chapter 1:

General Introduction

1.1 Preface

Subjective experience suggests that attention plays an important role in shaping perceptual awareness. This can become particularly apparent in situations that place extreme demands on attention. Landing a plane, for example, requires a great deal of concentration. Pilots have to monitor speed, altitude, wind direction and many other factors. Highly trained pilots can cope with these demands, but are not infallible. When experienced pilots 'landed' an aircraft in a flight simulator, and on some approaches were suddenly presented with the image of a large aircraft obstructing the runway – one in four pilots failed to notice the obstacle, simply landing through it (Haines, 1991). This example illustrates two fundamental properties of the visual system. First, its limited capacity for processing information, and second, its selectivity (e.g. Broadbent, 1958). Complex visual scenes are often cluttered with many different stimuli. At any given time, only a fraction of the information received from the retina can be selected for further processing and used to control behaviour. Furthermore, as I discuss below, despite our subjective impression that our visual experience is a full, rich representation of the world around us, not all stimuli with which we are presented – not even all behaviourally relevant ones – actually reach awareness (O'Regan & Noe, 2001; Simons & Rensink, 2005).

What factors determine conscious visual experience? In recent years there has been a growing interest in perceptual awareness within cognitive neuroscience. Research in this area has attempted to characterize the cognitive and neural mechanisms that mediate awareness (Baars, 1988; 1997; Crick & Koch, 2003; Driver & Mattingley, 1998; Kanwisher, 2001; Naghavi & Nyberg,

2005; Posner, 1994; Rees, Kreiman & Koch, 2002; Rees & Lavie, 2001). Behavioural and neural evidence suggests that awareness is intimately related to cognitive functions such as attention. However, the cognitive mechanisms and the neural substrates of top-down influences on awareness require further elucidation. In this thesis I investigate the relationship between visual awareness and top-down cognitive functions, examining the extent to which these functions determine conscious perception. This investigation is guided by Lavie's load theory of selective attention and cognitive control (Lavie, 1995; 2005; Lavie, Hirst, De Fockert & Viding, 2004).

Load theory proposes that perception has limited capacity but proceeds automatically on all stimuli (whether relevant to the task at hand or not) until capacity is exhausted (Lavie, 1995). It also proposes that executive control functions such as working memory are responsible for the allocation of processing resources to certain stimuli over others (Lavie et al, 2004; Lavie, 2005). The idea that attention is generated by executive control has been stipulated previously (e.g. Baddeley, 1996; Desimone & Duncan, 1995). Load theory, however, proposes a specific role for working memory in the control in selective attention, that of maintaining stimulus processing priorities.

A fundamental prediction of load theory is that increasing the perceptual load of a task will consume capacity, therefore reducing processing (and awareness) of stimuli external to that task (Lavie, 1995). However, nearly all previous evidence supporting this hypothesis has been based on indirect measures of perceptual processing, such as reaction times (Beck & Lavie, 2005; Lavie, 1995; Lavie & Cox, 1997; Lavie & Fox, 2000) and neural activity (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Pinsk, Doniger, & Kastner 2003; Schwartz et al,

2005; Rees, Frith & Lavie, 1997; Yi, Woodman, Widders, Marois, & Chun, 2004) in selective attention tasks, rather than direct assessments of awareness.

The suggestion that working memory serves to maintain stimulus processing priorities leads to the prediction that exhausting working memory will reduce executive control of attention, and will therefore results in increased processing (and awareness) of ignored stimuli (Lavie, et al, 2004; Lavie, 2005). This prediction has also received empirical support, from studies showing that loading working memory increases interference from irrelevant distractors, as measured by reaction times (De Fockert, Rees, Frith & Lavie, 2001; Lavie & De Fockert, 2005; Lavie et al, 2004) and neural activity (De Fockert et.al, 2001) in Stroop-like and attentional capture tasks.

But perceptual processing does not necessarily imply conscious awareness of stimuli – it can occur in the absence of awareness (Dehaene et al, 1998; Driver & Mattingley, 1998; Marshall & Halligan, 1988; Rees & Frith, 1997; Rees et al, 2000). Here I will describe experiments that employed manipulations of perceptual load (in Chapters 2 and 3) and working memory load (in Chapter 5) to examine whether the predictions derived from load theory generalize to conscious visual perception – the reported, subjective experience of a visual percept. The involvement of a high-level network of frontal and parietal brain regions in visual awareness was investigated in a neuroimaging study (Chapter 4), and the causal role of right parietal cortex in resolving competitive interactions in visual awareness was examined using Transcranial Magnetic Stimulation (TMS; Chapter 5).

In the next sections I briefly review the research that prompted the questions addressed in this thesis. I begin with the debate regarding the locus of selection

in visual attention. This is followed by a description of load theory, which offers a resolution to the debate, and an examination of the experimental evidence supporting load theory to date. I then outline of the evidence for the effects of different types of load on awareness, and various criticisms of this evidence that I address in the research presented in this thesis.

1.2 Early versus late selection in visual attention and awareness

When attention is directed towards certain stimuli, to what extent are unattended stimuli perceived? This question has been the focus of a long-standing debate in the selective attention literature. On the one hand, proponents of *early selection* (e.g., Broadbent, 1958; Treisman, 1969) suggest that attention serves a perceptual system whose capacity is limited. Attention can therefore effectively prevent early perceptual processing of irrelevant, or ignored, information, and perception is restricted to attended items. On the other hand, the *late selection* viewpoint (e.g., Deutch & Deutch, 1963; Duncan, 1980) proposes that perception is an automatic (i.e. effortless, limitless in capacity and involuntary) process, which proceeds on all stimuli regardless of their task relevance. Attention, according to this view, can only affect post-perceptual processing stages such as response selection or memory. The debate's longevity is due to the fact that substantial empirical support has been found for both points of view. In fact, as late as 1993 it was still suggested that the contradictions thrown up by this research may never be resolved (Allport, 1993).

1.2.1 Evidence favouring early selection

A large body of research indicates that focusing attention on task-relevant information can significantly reduce – even completely eliminate – knowledge of simultaneously-presented irrelevant information. Early studies of the auditory modality employed the dichotic listening method, in which participants selectively attend to one of two streams of words, each presented to a different ear. These studies showed that participants were later unable to report unattended information (Cherry, 1953; Moray, 1959). Analogous research in the visual domain used the selective reading paradigm to show that when participants read a text printed in a particular colour while ignoring text in a different colour printed in alternating lines, they were later unable to report the ignored text (Neisser, 1969).

To counter the criticism that the generality of the conclusions drawn from the above examples may be limited due to their use of complex verbal material, researchers employed various versions of a (non-verbal) selective looking paradigm. For example, participants were required to make aesthetic judgments on a stream of objects that crossed the screen in one direction, while ignoring an overlapping stream moving in the other direction. When later given an unexpected recognition test, they were at chance in identifying ignored objects (Rock, Shauer & Halper, 1976).

In a static version of the same task, participants attended to one of two superimposed images (distinguished by their colour), and later recognized attended (but not unattended) images above chance level when given a surprise recognition test (Goldstein & Fink, 1981; Rock & Gutman, 1981). A similar

paradigm was used in a more recent neuroimaging study (Rees, Russell, Frith & Driver, 1999), in which participants were presented with a rapid, fixated stream of words and meaningless letter strings, each superimposed on a line drawing. Participants were instructed to attend to either the drawings or the letters, and to detect immediate repetitions of stimuli within the attended stream. Similarly to previous studies, a later recognition test showed that memory for unattended words was significantly impaired compared to attended words (in fact, correct identification of unattended words was indistinguishable from erroneous false alarms for 'foil' words not presented during scanning, indicating that the unattended words were not remembered at all). Furthermore, when attending to drawings, participants' brain activity no longer differentiated between meaningful words and meaningless letter strings (as it did when letters were attended), indicating that unattended words may not have been processed despite clearly appearing at fixation (**Figure 1.1**).

The selective looking paradigm was also used in studies presenting lengthy real-life scenes. In a number of studies (Becklen & Cervone, 1983; Neisser & Becklen, 1975; Littman & Becklen, 1976), researchers superimposed two video-clips and instructed participants to attend to one of them (e.g. by counting the number of passes a team throwing a ball around made). When later questioned, participants showed no knowledge of unexpected and unusual events occurring in the unattended clip, such as a woman with an umbrella walking across the screen, or a change in the kind of activity taking place. The possibility that eye-movements could account for this effect (e.g. due to blurring of unattended stimuli as attended stimuli were tracked) was ruled out in one study (Littman & Becklen, 1976), where eye position was monitored to ensure that gaze was

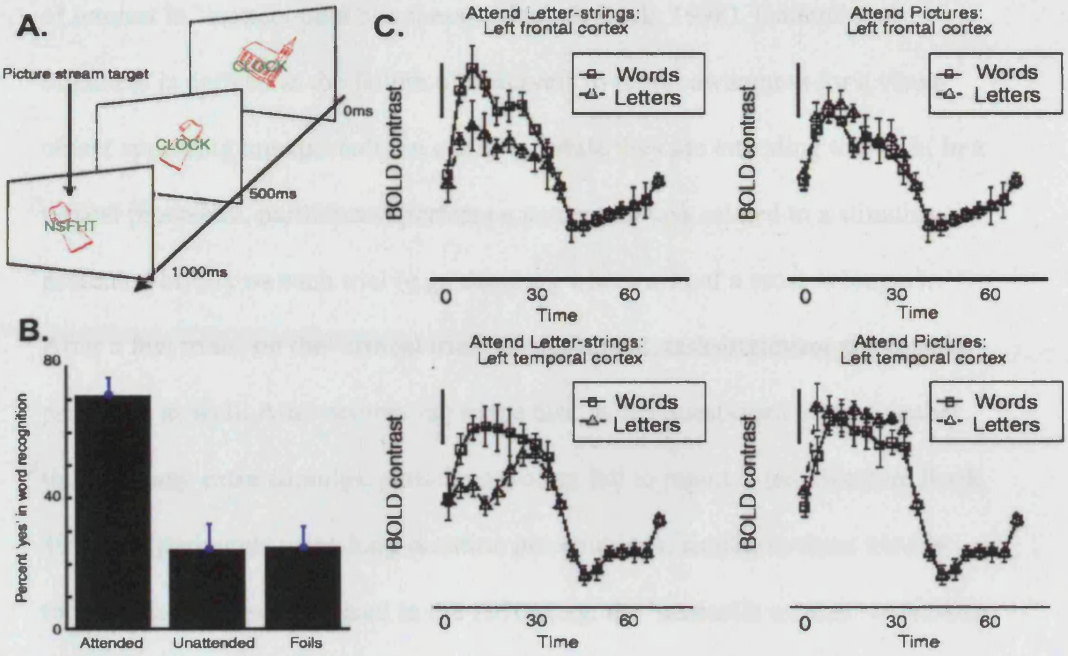

Figure 1.1. No perception of words when attending to superimposed drawings. (A) Stimuli used in Rees et al (1999). Common nouns or word strings were superimposed on line drawings, and such displays were shown at 500 ms intervals, for 250 ms each. Participants detected immediate repetitions, either in the letter or drawing stimuli. (B) Percentages of 'yes' responses in a post-scanning recognition memory test. When presented with test words, participants were likely to recognize words attended during scanning, but equally likely to say they remembered unattended words as they were to 'remember' foil words that had not been presented beforehand. (C) Time course of Blood-Oxygen-Level-Dependent (BOLD) activation foci in left frontal (upper panels) and left posterior basal temporal cortex (lower panels). Unshaded regions (left half of each panel) show activation during task performance, and shaded areas (right) show activation during a passive fixation baseline. The brain regions whose time courses are shown here were those which showed the greatest differentiation between meaningful words and meaningless letter strings when letters were attended (left two panels). These differences, however, were abolished when participants attended to the drawings. Adapted from Rees et al (1999).

maintained at fixation.

The use of displays in which an unexpected (and often unnoticed) event occurs has been revived in a recent series of studies, as part of a renewed surge

of interest in 'inattentional blindness' (Mack & Rock, 1998). Inattentional blindness is defined as the failure of observers to report awareness for a visual object appearing unexpectedly in a display while they are attending to a task. In a typical procedure, participants perform a perceptual task related to a stimulus presented briefly on each trial (e.g., deciding which arm of a cross is longer). After a few trials, on the 'critical trial', an additional, task-irrelevant stimulus is presented as well. After responding to the task, when questioned about whether they saw any extra stimulus, participants often fail to report it (see Mack & Rock, 1998). Experiments using long-duration presentations, similar to those used in the original studies performed in the 1970s (e.g. the 'umbrella woman' in Neisser & Becklen, 1975), are now known as studies of 'sustained' inattentional blindness (Most, Simons, Scholl & Chabris, 1998). In addition to replicating the findings from the early studies, such new studies have found that it was unnecessary to superimpose two semi-transparent video clips, indicating that the effect was not due to the unusual, degraded appearance of such films: Simons & Chabris (1999) showed participants a single clip, in which two teams – one wearing white shirts, the other black – passed balls between members of the same team. While participants monitored one of the games (by counting passes), a person in a gorilla suit walked across the screen. When asked at the end of the clip, participants often failed to report the gorilla (**Figure 1.2**). The same type of effect has also been shown to occur when simpler, highly controlled displays were used. In one study (Most et al, 2001), participants monitored a set of randomly-moving shapes (black letters) for the number of times they bounced off the edge of the screen, while ignoring a different set of shapes (white letters).

Figure 1.2. The unnoticed gorilla. A single frame from the video clip used by Simons & Chabris (1999). While participants monitored either the white- or black-shirt team, a man in a gorilla suit walked across the screen, banged his chest (as seen here) and continued walking until exiting from the other side. When questioned at the end of the 25-second clip, participants often failed to report the gorilla, despite it being perfectly visible for 9 seconds.

They often failed to notice an unexpected shape (a grey cross) entering the screen and crossing it horizontally until it exited on the other side.

The evidence reviewed so far seems to indicate that selective attention can prevent perceptual processing and awareness of stimuli irrelevant to the task at hand, thus lending support to the early selection view. However, there is also a considerable amount of experimental work supporting the opposite position.

1.2.2 Evidence favouring late selection

Research bolstering the late selection view has employed diverse experimental methods, most of which are variations of the classic Stroop paradigm (Stroop, 1935). Rather than asking participants whether they remember unattended items, as in most studies supporting early selection, such research has usually utilized indirect measures of perceptual processing, such as the effects unattended stimuli have on target RTs.

In the classic Stroop paradigm, participants are required to report a particular attribute of a stimulus. The stimulus also contains information in a different dimension that is either congruent or incongruent with the correct response. For example, in the colour-word Stroop task participants are shown a colour name printed in a colour which may be the same (e.g. RED) or different (e.g. RED) from the one the colour name denotes. Participants required to make a speeded response, reporting the ink colour, have been found to be faster and make fewer mistakes when the ink and name are congruent than when they are incongruent (Stroop, 1935). The fact that the irrelevant dimension affects responses to the relevant one indicates that it is processed to the level of semantic meaning despite its irrelevance. This effect could thus be construed as representing late selection.

However, in Stroop tasks both the relevant and irrelevant information reside within the same stimulus, occupying the same spatial location. Furthermore, different attributes of the same object are known to enjoy a processing advantage (compared to similar attributes belonging to different objects; Baylis & Driver, 1993; Duncan, 1984). Thus, the fact that the irrelevant dimension could not be

ignored may not generalize to other cases in which distractors are presented.

Congruency effects are still found, though, in spatially-separated versions of the classic word-colour Stroop task, using separate target colour patches and distractor colour-names (printed in black ink), and varying the distance between them (Gatti & Egeth, 1978; Hagenaar & van der Heijden, 1986; Merikle & Gorewich, 1979). Similarly, interference from incongruent (compared to congruent or neutral) emotional faces has been found when the task was to categorize words superimposed on them as positive or negative (Stenberg, Wiking & Dahl, 1998).

A different method in which targets and distractors are separate is known as the flanker paradigm (e.g., Eriksen & Eriksen, 1974). In flanker experiments, a choice response to a centrally-presented target must be made (e.g., reporting whether a letter appearing somewhere along the screen's horizontal meridian is, for example, an H or a K) while distractors appearing in different, peripheral spatial locations (e.g., above or below the horizontal meridian) are ignored. The distractors may be congruent or incongruent with the target (for example, a peripheral H would be congruent with a target H, and incongruent with a target K), or they may be neutral (for example, the letter Y). The result is known as the flanker effect (Eriksen & Eriksen, 1974; Miller, 1987). Target RTs are typically slower when accompanied by incongruent than by congruent or neutral distractors, indicating that despite knowing where the target would appear, participants are not able to ignore the irrelevant information, which is processed to a level at which it affects behaviour. Furthermore, the flanker effect is still found when the spatial separation between targets and distractors is increased (Eriksen & Eriksen, 1974; Flowers & Willcox, 1982; Miller, 1987), even when

the distance is as large as 6° (Murphy & Eriksen, 1987). Though the interference from distractors is reduced as their distance from targets increases, this trend can be abolished if distractors and targets are perceptually grouped by being connected (Kramer & Jacobson, 1991), or having similar motion trajectories (Driver & Baylis, 1989) or colour (Baylis & Driver, 1992).

Flanker effects have also been observed when the target and distractor were separated not only in space, but in time as well (i.e. when there was a temporal delay between distractor and target), as long as the distractor did not appear later than the target (Flowers & Wilcox, 1982; Gathercole & Broadbent, 1987). Finally, distractors can become incongruent with targets despite not being initially associated with the alternative response, simply as a result of being repeatedly paired with a different target (Miller, 1987), demonstrating that associative learning related to ignored stimuli can occur.

Another finding supporting late selection is the phenomenon of negative priming (Tipper, 1985). If a target has served as a distractor in a previous trial, RTs to it will be longer than if it has not. This occurs even if distractors and targets are presented in different symbolic domains (e.g., distractors as pictures and targets as words; Tipper & Driver, 1988), indicating that distractors are not only perceived but are processed to an abstract semantic level so that a categorical representation, rather than simply a crude structural description, is created (Tipper, 1985).

1.2.3 Discrepancies and failed resolutions

A great deal of empirical evidence seems therefore to support each of the two sides in the debate regarding the locus of attentional selection. How can these conflicting experimental results be resolved?

It is worth noting that most paradigms used in research supporting the early selection view require participants to remember and explicitly report the presence of irrelevant stimuli after they have disappeared. Conversely, most research supporting the late selection position used paradigms in which processing of irrelevant distractors was assessed online, through indirect effects on task performance. Could the methodological differences between the experimental paradigms used in each strand of research account for the different results obtained in them?

One possibility is that due to the temporal delay between exposure to the stimuli and being asked about them, early selection results obtained with paradigms such as selective looking actually reflect a failure of memory rather than one of awareness or of perceptual processing. Though this proposal makes sense logically, it seems very unlikely that participants could be fully aware of unusual events lasting several seconds (e.g., a gorilla crossing the screen for 9 of the 25-second presentation in Simons & Chabris, 1999), yet completely forget them by the time they are prompted to report them a few seconds later.

A different account distinguishes awareness from perceptual processing. Perhaps irrelevant information is perceived and processed, but does not reach awareness. Therefore, when participants are explicitly asked about task-irrelevant stimuli of which they are unaware, they are unable to report anything about them

(as in the research supporting early selection). However, in tasks where response conflict could arise (as in the research supporting late selection), the unconscious processing of task-irrelevant stimuli leads to measurable effects.

Unfortunately, this account also seems unlikely, as it depends heavily on the methodological distinction between paradigms that explicitly assess awareness and those that indirectly assess perceptual processing. According to this explanation, the former kind should always lead to results supporting early selection, whereas the latter should consistently lead to results supporting late selection. This, however, is not the case. The paradigms typically yielding results showing no awareness of irrelevant stimuli have occasionally shown that unattended information does indeed reach awareness – as occurs, for example, when participants hear their own name in an unattended auditory stream of words (the cocktail party effect; Cherry, 1953).

Similarly, a variety of factors modulating the rates of inattentional blindness has been identified. These include the size of the unattended stimulus (Mack & Rock, 1998), its position relative to the target (Most et al, 1998; Newby & Rock, 1998), and its salience (Mack & Rock, 1998), as well as the attentional set of participants (Most, Scholl, Clifford & Simons, 2005). Such findings indicate that unattended visual stimuli can indeed reach awareness under certain conditions.

Conversely, though the results of most response-conflict studies have supported late selection, some have shown no effect of distractors (consistent with early selection). In the flanker paradigm, the effect of distractors is significantly reduced when they are 'diluted' in displays containing an additional distractor (Jenkins, Lavie & Driver, 2003), and effective cuing towards targets nearly eliminates distractor interference (Eriksen & Hoffman, 1972, 1973; Yantis

& Johnston, 1990). Similarly, in the spatially-separated Stroop task adding a response-neutral stimulus (a word or row of 'X's) to the display strongly reduces the effects of distractors (Brown, Gore & Carr, 2002; Kahneman & Chajczyk, 1983). Finally, negative priming is eliminated when the exact location of the target in a letter-identification task is known (Ruthruff & Miller, 1995).

These discrepancies demonstrate that the differences in the findings of studies supporting early and late selection cannot be attributed to purely methodological considerations, such as the differences between indirect measures and explicit retrospective measures. Indeed, discrepancies have been found between studies using the same tasks. A different theoretical approach, accounting for evidence of both early and late selection within the same experimental paradigms, is clearly needed.

1.3 Load theory: A resolution to the debate

In a series of studies, Lavie and colleagues (Lavie & Tsal, 1994; Lavie, 1995, 2000, 2001; Lavie et. al., 2004) have proposed a hybrid model, which combines aspects of both the early and late selection viewpoints and accounts for the contradictory results found in earlier research. Lavie's load theory of selective attention and cognitive control not only allows a reinterpretation of previous experimental work, but gives rise to novel empirically-testable predictions. In this section I describe the theory and the new empirical evidence supporting it with regard to perceptual processing and attentional selection. In the next section

I outline the remaining open questions concerning the implications of load theory for awareness.

1.3.1 Theory, definitions and predictions

Load theory synthesises the early and late selection approaches by making two central assumptions: The first is that the perceptual system does indeed have limited capacity (as proposed by early selection). The second, however, is that all stimuli, regardless of their relevance to the task at hand, are processed automatically (as in late selection) – but only until perceptual capacity is exhausted (Lavie & Tsal, 1994; Lavie, 1995).

From these assumptions load theory proceeds to postulate two mechanisms of selective attention. First, a relatively passive selection mechanism in which the level of perceptual load determines the degree to which irrelevant distractor stimuli will be excluded from perception. When the level of perceptual load involved in processing task-relevant stimuli is sufficiently high to exhaust perceptual capacity, no capacity remains for processing of distractors, leading to their exclusion from perception. Therefore, in situations of high perceptual load early selection will occur and distractor interference will be prevented. If, however, the perceptual load imposed by the task at hand is low and does not exhaust capacity, any residual capacity will 'spill over' and lead to mandatory processing of irrelevant distractors. Low perceptual load will therefore result in late selection, thus enabling distractor interference (Lavie, 1995; 2000; 2001).

The second mechanism is an active attentional control mechanism determining stimulus processing priorities, e.g. between targets and irrelevant

distractors. The importance of such active control is immediately apparent in situations where irrelevant stimuli are perceived and can compete with relevant stimuli for further processing and control of behaviour (i.e. under low perceptual load, when late selection occurs). This requires an active control process, to ensure that both the choice of stimuli for further processing (beyond initial perception) and eventual response selection are in line with current behavioural goals. Load theory proposes that this kind of control depends on high-level cognitive functions such as working memory, which are required to actively maintain current processing priorities. Critically, this proposed mechanism predicts that high working memory load should have an opposite effect to that obtained under high perceptual load. Exhausting the capacity of active cognitive control functions should reduce the ability to maintain prioritization of current behavioural goals, leading to more (rather than less, as under high perceptual load) processing of irrelevant distractors (Lavie et. al., 2004; Lavie, 2005).

The two mechanisms involved in selective attention are thus dissociable, and it should be possible to demonstrate this through the effects that different kinds of load will have on interference from irrelevant distractors. Load theory predicts that whereas perceptual load will decrease distractor interference, working memory load will increase it (when perceptual capacity is not exhausted).

Before proceeding, it is important to define the term 'load' for perception and working memory, in the context of load theory. An increase in *perceptual load* is conceptualized as either (a) an increase in the number of items in a display while performing the same task (e.g., increasing the search array in a visual search task), or (b) an increase in the perceptual demands of a task, while viewing the same display (e.g., making a response based on a conjunction of features rather

than a single attribute; Lavie, 1995; Treisman, 1988). The extra items presented or additional operations required under high perceptual load exhaust capacity, thus precluding processing of irrelevant stimuli.

Similarly, an increase in *working memory load* can be defined as either (a) an increase in the number of items to be maintained in working memory for the same period of time, while performing the same unrelated activities (e.g., remembering a single item versus remembering several items; Lavie et al, 2004), or (b) an increase in the demands that the task places on working memory for the same number of items (e.g., remembering the order of randomly-arranged items versus items always presented in the same order; De Fockert et. al., 2001; Lavie & De Fockert, 2005). The increase in working memory load reduces the ability of cognitive control functions to maintain prioritization of stimuli unrelated to the memory task, leading to increased processing of distractors.

The above definitions entail that what constitutes an 'item' must also be defined within any manipulation of perceptual or working memory load. This definition need not be absolute – for example, a string of letters could constitute a single item (a word) in one task, or several items (separate letters) in another. Therefore, whenever a manipulation of load involves varying the number of items, or keeping this number constant while varying task demands, it is important that items in the different experimental conditions are defined in the same way.

Finally, it is important to note that the opposite effects predicted by the theory for increases in perceptual and working memory load rule out any explanation of such effects in terms of increases in general task difficulty.

1.3.2 Evidence for load theory: Perceptual load

The selection mechanism proposed by load theory entails that the perceptual load imposed by a task determines the extent of distractor processing. Previous research on the locus of selective attention can be re-interpreted in light of this suggestion. In an extensive review of this literature, Lavie & Tsal (1994) showed that evidence of early selection was usually found in studies in which the task involved considerable perceptual load. For example, results indicating no distractor interference in response-competition paradigms (e.g., the flanker task; Yantis & Johnston, 1990; or the spatially-separated Stroop task; Kahneman & Chajczyk, 1983) occurred when the task involved a large number of stimuli in each display. As load theory predicts, this could lead to an exhaustion of perceptual capacity and therefore reduce distractor interference.

Conversely, in the more common case of studies that did find distractor interference using these paradigms (e.g., Eriksen & Eriksen, 1974 in the flanker task; Gatti & Egeth, 1978; and Hagenaar et al, 1986 in Stroop tasks), the display usually consisted of a single target and single distractor. Such low perceptual load would leave enough spare capacity for the irrelevant distractor to be perceived, processed, and affect behaviour.

Lavie and Tsal (1994) focused their review on flanker tasks and the effects of load via increased set size, but in a similar manner it could be argued that selective looking and sustained inattentional blindness paradigms have employed tasks characterized by high perceptual load, leading to results supporting early selection. These paradigms usually required participants to follow multiple targets moving in a random fashion (e.g., Neisser & Becklen, 1975; Simons &

Chabris, 1999), or monitor rapidly-alternating targets (e.g., Rees et al, 1999).

Accounting for the previous literature in terms of load theory, however, does not in itself provide sufficient support for the theory. Perceptual load was not directly manipulated in any of the previous studies, making it possible to attribute the discrepancies in findings to alternative factors. The reduction in distractor interference when the number of irrelevant stimuli was large could be attributed, for example, to a reduction in the salience of response-relevant distractors under conditions of increased display clutter, rather than to the exhaustion of perceptual capacity under high perceptual load.

Therefore, in a series of studies Lavie and colleagues directly manipulated perceptual load, and measured the effect this had on processing of irrelevant distractors. Using the flanker paradigm, perceptual load was varied by changing the number of items in the attended set (Lavie, 1995; Lavie & Cox, 1997). Participants searched for a target letter, deciding whether it was an X or an N on each trial. The target could appear in one of six pre-defined locations. Under low load it could either appear alone (Lavie, 1995) or accompanied by the letter 'O' in all other locations (Lavie & Cox, 1997). Under high load, the other five relevant locations were occupied by non-target angular letters that were dissimilar to each other. Distractor letters, which were to be ignored and could be either congruent or incongruent with the target, appeared in the periphery (see **Figure 1.3a**). Results supported the predictions of load theory. Under low perceptual load, response conflict due to distractor interference was evident – RTs in trials with an incongruent distractor were significantly longer than in

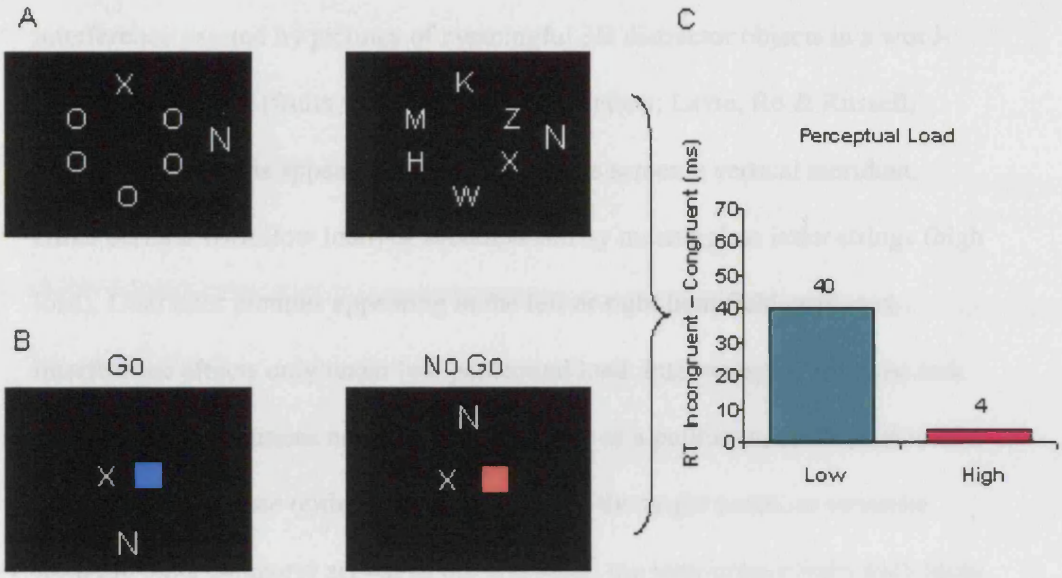

Figure 1.3. Manipulations of perceptual load in the flanker task and their effect on distractor processing. In these tasks, participants make a speeded response, indicating which of two target letters (X or N) appears in one of several pre-defined locations while trying to ignore an irrelevant distractor. Distractor interference (and therefore processing) is indicated by slower responses in the presence of an incongruent compared with a congruent distractor. (A) Perceptual load is manipulated by changing the number of non-target items in relevant locations that are similar to the target (angular) and dissimilar to each other, from none under low load (left), to five under high load (right). The distractor appears outside the circle of relevant locations (Lavie & Cox, 1997). (B) Perceptual load is manipulated by increasing the processing requirements for the same displays. Under low load the presence of any blue shape indicates 'go' – a response to the target should be made (the other colour, red, indicates 'no go'). Under high load stimulus conjunctions (e.g., blue square *or* red circle) indicate 'go' (Lavie, 1995). (C) Distractor interference effects (incongruent minus congruent RTs) are greater under low than under high perceptual load. Adapted from Lavie, 2005.

trials with a congruent one. Under high perceptual load, however, such differences were eliminated, indicating that distractors had not been processed (**Figure 1.3c**). A similar effect of perceptual load was found when distractors

were presented at fixation (Beck & Lavie, 2005). They were also found for interference exerted by pictures of meaningful 3D distractor objects in a word-categorization task (fruits versus musical instruments; Lavie, Ro & Russell, 2003). Target words appeared somewhere on the screen's vertical meridian, either on their own (low load) or accompanied by meaningless letter strings (high load). Distractor pictures appearing in the left or right hemifield produced interference effects only under low perceptual load. Interestingly, when the task was to classify a famous name as either a singer or a politician, and a picture of a famous person's face (either the same person as the target name, or someone from the other category) served as the distractor, the interference from such faces was not modulated by perceptual load. Similarly, covert priming (faster identification following previous exposure) to task-irrelevant famous faces was not modulated by the perceptual load of the task carried out during initial exposure to the faces (Jenkins, Burton & Ellis, 2002). This could indicate that faces are unique, drawing perceptual resources in a mandatory manner regardless of the task, perhaps due to their social significance. On the other hand, the social significance of faces might just imply that higher levels of perceptual load are required to modulate their processing (e.g., Pessoa et al, 2002).

The manipulations of perceptual load described above varied the number of items in relevant locations in the display. The condition of high and low load thus differed in their physical appearance as well as the demands they made on attention. Other experiments (Lavie, 1995) therefore invoked the second definition of perceptual load, as described in the previous section, employing identical displays in all conditions while varying task demands. Distractor interference effects were measured while participants performed a task in which

the correct response was determined either by a single stimulus feature (low load) or a conjunction of features (high load, see **Figure 1.3b**); alternatively, perceptual load was manipulated for identical displays by using a demanding position and size discrimination (high load) versus a simple detection of presence (low load). Again, results showed that distractors exerted greater interference under low (compared to high) perceptual load.

Manipulating perceptual load was also shown to affect implicit learning of the spatial configuration of irrelevant distractors (Jiang & Chun, 2001), as well as negative priming (the slowing of responses to targets previously presented as distractors; Tipper, 1985). Lavie & Fox (2000) found that increasing the number of items in relevant locations of a display not only decreased interference from concurrently-displayed distractors, but also eliminated the negative priming effect (which was present under low perceptual load) when such distractors were later used as targets. Negative priming is considered to indicate active inhibition of distractors (Allport, Tipper & Chmiel, 1985). Therefore, it is unlikely that the reduction in distractor interference found in the above studies was due to an increase in distractor inhibition under high perceptual load. Rather, these results are more consistent with an attenuation of distractor perception under high load.

Evidence from neuroimaging studies also converges on the same conclusion. Neural activity in stimulus-sensitive brain regions has been shown to decrease under high (compared to low) perceptual load, when the specific stimulus these regions respond to preferentially was task-irrelevant. Rees et al (1997) measured brain activity with fMRI while participants performed a linguistic task, either deciding whether words appearing at fixation were printed in lower or UPPER case (low load) or how many syllables they contained (high load). An irrelevant

motion stimulus was presented in the periphery concurrently with the fixated words. Rees et al (1997) found activation in the motion-sensitive area MT+/V5 under low perceptual load, but not under high load. Similarly, Yi et al (2004) presented irrelevant pictures of places in the periphery while participants performed a repetition-detection task for faces presented at fixation. They found that activity in the place-sensitive parahippocampal place area (Epstein & Kanwisher, 1998) was significantly reduced when the face task was made more difficult. Moreover, repetition suppression (attenuation of the fMRI signal when a stimulus is repeated; Grill-Spector & Malach, 2001) was only found in the parahippocampus for peripheral images of places under low load in the face task, indicating that processing of the irrelevant stimuli under high load was reduced to the extent that repetition was not detected. Modulation by perceptual load of activity in the colour-sensitive region V4 has also been demonstrated. Increasing load related to a target presented in one hemifield reduced activity related to colourful images presented in the other hemifield (Pinsk et al, 2003). In a different study, activation in the amygdala in response to attended emotional (angry, fearful or happy, compared to neutral) faces was abolished when participants attended to a demanding orientation-discrimination task (Pessoa et al, 2002). This shows that activity not only in cortical, but in subcortical regions such as the amygdala can also be modulated by perceptual load, and challenges previous claims that amygdala responses to emotional stimuli do not require attention (Vuilleumier, Armony, Driver & Dolan, 2001), suggesting instead that previous failures to find attentional modulation of amygdala activity were due to the use of tasks that did not place sufficient load on perceptual capacity.

Modulation of neural activity has been found not only in stimulus-selective brain regions, but also in early visual cortex. Schwartz et al (2005) measured retinotopic visual cortex activity evoked by checkerboard patterns presented in the periphery while participants performed a task related to a rapid stream of stimuli presented at fixation. The task was performed under either low or high perceptual load (**Figure 1.4a**). Visual cortex activity evoked by the task-irrelevant checkerboards was reduced under high load. This effect was found in areas V1, V2, V3 and ventral V4. Though the magnitude of the effect increased with successive visual areas, it was clearly present as early as V1 (**Figure 1.4b**).

An event-related potentials (ERP) study also supports the suggestion that perceptual load can modulate activity related to task-irrelevant stimuli in early visual cortex (Handy, Soltani & Mangun, 2001). This study found that compared to low load (simple feature detection), high perceptual load (harder letter discrimination) reduced the amplitude of the occipital ERP component P1 evoked by irrelevant distractors. The P1 occurs 80-130 ms after stimulus presentation, and is believed to reflect early sensory processing. Another similar fMRI result was obtained by O'Connor, Fukui, Pinsk & Kastner (2002), who in addition to showing a reduction in V1-V4 activity under high perceptual load, also showed that compared to a low load task (monitoring for a colour change in a rapid stream of fixated stimuli), a high load task (monitoring for letters among other characters in the stream) caused a reduction in activity in the lateral geniculate nucleus (LGN) evoked by irrelevant peripheral visual stimulation. The LGN is often viewed as the main gateway passing visual information on to visual cortex. To date, no feedback connections to earlier stages of the visual pathways

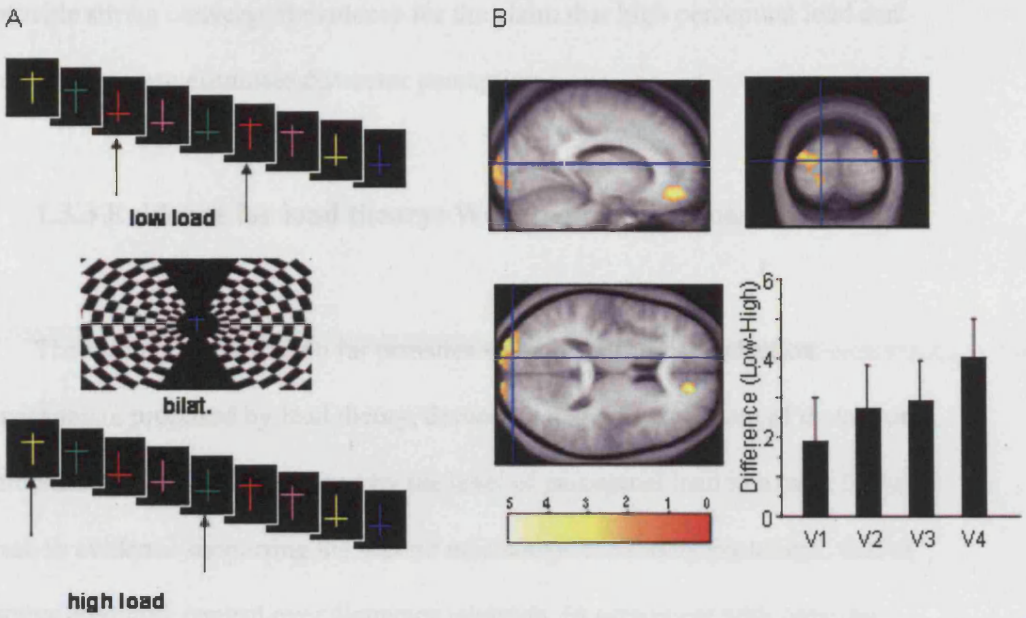

Figure 1.4. The effect of perceptual load on retinotopic visual cortex activity evoked by irrelevant stimuli. Stimuli and results in Schwartz et al (2005). (A) Stimuli: A rapid stream of coloured crosses was presented at fixation, and participants monitored for targets defined at the beginning of each stream. Under low load, targets were defined by a single feature (colour; red crosses). Under high load, targets were defined by a conjunction of features (colour and orientation; upright yellow *or* inverted green crosses). Irrelevant contrast-reversing checkerboards were presented in the periphery either bilaterally (shown), on one side or on neither side. (B) Results: Visual cortex activity evoked by the checkerboards (pooled across unilateral and bilateral conditions, contrasted with the no-checkerboard condition) is greater under low than under high perceptual load in the central task. The bar chart shows that the difference increases monotonically from visual area V1 to V4. Adapted from Schwartz et al (2005).

(i.e. the optic chiasm and retina) have been discovered in mammals. Perceptual load may therefore affect visual processing at the earliest point in the visual pathway that top-down signals could possibly reach.

The studies reviewed above used various manipulations of perceptual load and various measures of distractor processing. Taken together, they therefore

provide strong convergent evidence for the claim that high perceptual load can reduce and even eliminate distractor perception.

1.3.3 Evidence for load theory: Working memory load

The research reviewed so far provides support for the first selection mechanism proposed by load theory, demonstrating that the extent of distractor processing is indeed determined by the level of perceptual load in a task. I now turn to evidence supporting the second mechanism the theory postulates, that of active cognitive control over distractor rejection. In agreement with previous suggestions (e.g., Desimone & Duncan, 1995), that working memory is required to successfully resolve competition according to current perceptual preferences, load theory (Lavie et al, 2004; Lavie, 2005) proposes specifically that high level cognitive control functions such as working memory maintain prioritisation (between relevant targets and irrelevant distractors) of current behavioural goals. Loading working memory should therefore reduce the cognitive system's ability to exert such control, leading to increased (rather than decreased, as in perceptual load) interference from irrelevant distractors competing with targets for processing.

Some evidence regarding the role working memory plays as a top-down control mechanism, defining and maintaining the bias between competing visual stimuli, has come from single-unit research. A number of studies (Fuster & Jervey, 1981; Miller, Li & Desimone, 1993; Miyashita & Chang, 1988) found cue- or template-related activity in monkeys' inferior temporal (IT) cortex – a region associated with working memory (Chelazzi, Miller, Duncan & Desimone,

1993) – during delay periods before the appearance of visual stimuli. Enhanced responses to targets matching a prior cue have also been found in the same area (Miller & Desimone, 1994). Activity in frontal cortex has also been associated with working memory (Courtney, Ungerleider, Keil & Haxby, 1997; D'Esposito & Postle, 2000; Goldman-Rakic & Friedman, 1991) and indeed, electrophysiological studies (Miller, Erickson & Desimone, 1996; Rainer, Asaad & Miller, 1998) found prefrontal neurons involved in the maintenance of task relevant information.

Findings regarding the maintenance of task requirements in frontal cortex were also obtained using fMRI: During a delay between task instructions and stimulus onset, anterior prefrontal cortex was activated. In addition, depending on the kind of task used, either verbal or spatial processing areas in the posterior prefrontal lobe were active during the delay (Sakai & Passingham, 2003). In themselves, these results do not mean that neurons in those regions exert top-down control, but they do imply that activity associated with working memory is relevant to visual tasks.

Another line of evidence suggesting the involvement of frontal cortex in biasing visual processing in humans has come from neuropsychological reports of selective attention deficits following frontal lobe damage (e.g., Shallice & Burgess, 1991). Such patients appear to be particularly distracted by dominant but goal-irrelevant distractors. Consistent with this, the process of aging has been associated with loss of cells in the brain, most notably in frontal cortex (e.g., Kramer, Humphrey, Larish, Logan & Strayer, 1994), and older adults have indeed been shown to exhibit higher rates of failure to inhibit irrelevant responses than young adults (e.g., Hasher & Zacks, 1988), a tendency which may

be associated with an aging-related deterioration in frontal lobe function. Support for this was found in a study (Maylor & Lavie, 1998), which showed increased distractor interference in old (compared to young) participants under low perceptual load, indicating that older participants were less able to inhibit interference from perceived distractors.

Evidence for the involvement of working memory in the cognitive control of selective attention has come from studies of individual differences that found a correlation between working memory span and performance in selective attention tasks. For example, Conway, Cowan & Bunting (2001) found that when participants attended to one of two auditory streams in a dichotic listening task, more low-span (65%) than high-span (20%) participants detected their name in the ignored channel (i.e. showed a cocktail party effect). Similarly, in another study low-span participants made more errors than high-span participants responding to incongruent words in a Stroop task (Kane & Engle, 2003), suggesting that people with a high working memory span are better able to focus attention on relevant information.

The evidence reviewed above is correlational, though, and until recently there has been little direct behavioural evidence in healthy humans for the causal role of working memory in the top-down control of attentional selection. A new series of studies (De Fockert et al, 2001; Lavie, 2000; Lavie et al, 2004; Lavie & De Fockert, 2005; Lavie & De Fockert, in press) has provided new insight into the way this system operates. These studies reduced the availability of working memory by loading it in a concurrent unrelated task. According to load theory, this should result in reduced ability to maintain task priorities, leading to greater interference from irrelevant distractors.

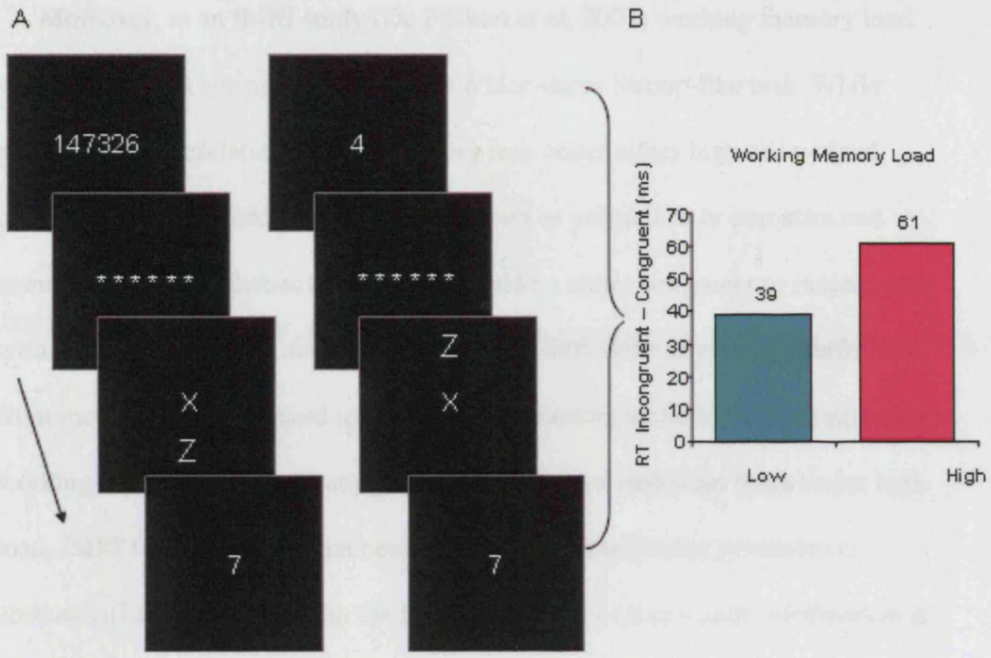

Figure 1.5. The behavioural effect of manipulating working memory load in the flanker task. (A) Working memory load was manipulated in Lavie et al (2004) by having participants remember a set comprising either one (low load) or six (high load) digits presented at the beginning of the trial. During the retention interval, participants performed a flanker task, identifying a central target letter while ignoring a peripheral distractor that could be either congruent or incongruent with the target. At the end of the trial participants responded to a probe digit, indicating whether it had been present or absent in the memory set. (B) Distractor interference effects (incongruent minus congruent RTs) are greater under high than under low working memory load, demonstrating that loading working memory leads to the opposite effect on distractor processing to perceptual load. Adapted from Lavie (2005).

This hypothesis was confirmed in behavioural experiments (Lavie et al, 2000; 2004). Working memory load was manipulated by having participants rehearse either a set of six digits (high load) or just one digit (low load; see **Figure 1.5a**). Distractor interference in the flanker task was significantly increased under high working memory load (**Figure 1.5b**).

Moreover, in an fMRI study (De Fockert et al, 2001) working memory load was manipulated during performance of a face-name Stroop-like task. While performing an unrelated working memory task under either high or low load, participants categorized famous written names as politicians or pop stars and attempted to ignore distractor faces that could be either congruent or incongruent with the name (**Figure 1.6a**). Behaviourally, results showed greater interference from incongruent (compared to congruent) distractors under high than under low working memory load, indicating more processing of distractor faces under high load. fMRI results showed that neural responses related to the presence (vs. absence) of a distractor face in the fusiform face area (Kanwisher, McDermott & Chun, 1997) were greater under high than under low working memory load (**Figure 1.6b**). These findings demonstrate that maintaining task-relevant perceptual biases depends on the availability of working memory for the control of goal-directed performance in a selective attention task.

The effects of working memory load are not restricted to control of visual selection in Stroop-like response-competition tasks. Lavie and De Fockert (2005) tested the effect of working memory load on attentional capture. Attentional capture occurs when one of the nontargets in a visual search array differs from others in a salient way, making it a unique 'singleton' on an irrelevant dimension (e.g. a red distractor among green stimuli in a shape-discrimination task). Such singletons tend to distract participants from the relevant stimuli, impairing performance on the search task (Theeuwes, 1991; 1992; Yantis, 1996; 2000). In line with the prediction of load theory, when working memory load was manipulated, attentional capture was exacerbated under high (versus low) load. This result is consistent with that of an fMRI study (De Fockert, Rees, Frith &

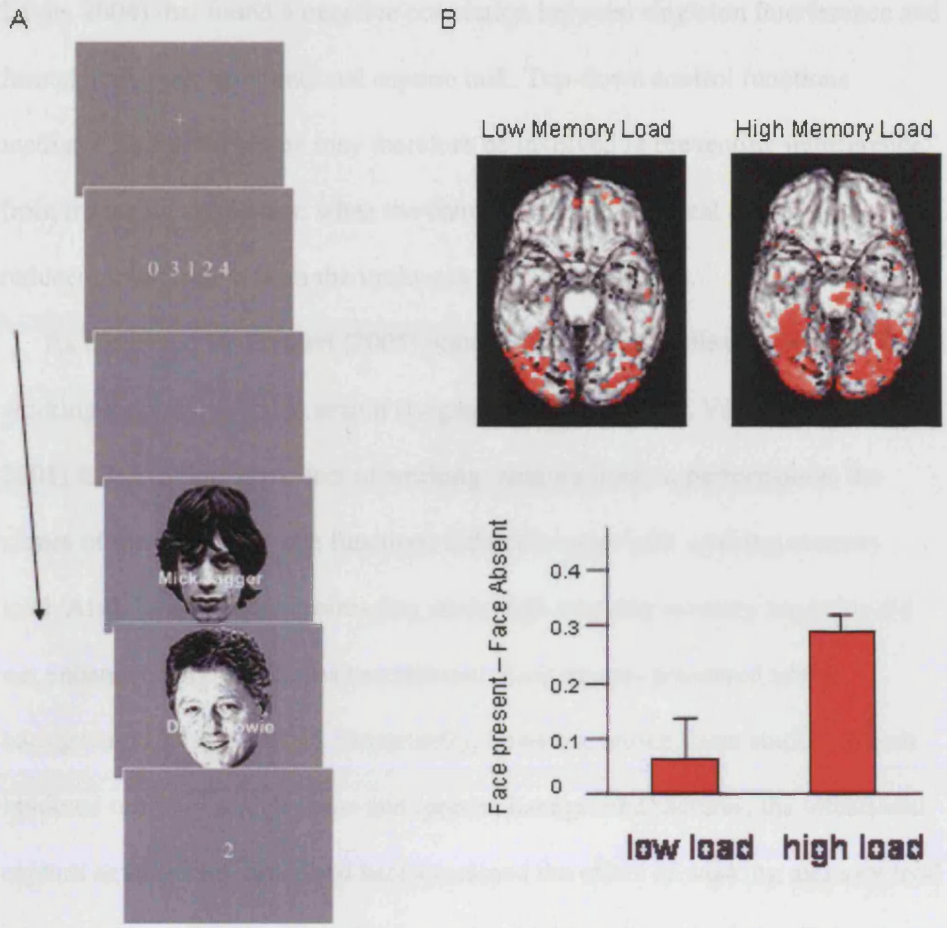

Figure 1.6. The effect of working memory load on face processing in a neuroimaging study. (A) Trial procedure and example stimuli used in De Fockert et al (2001). At the beginning of each trial, participants were presented with a set comprising the digits 0 to 4 in either a fixed ascending order (i.e. '01234', low load) or a random order (as shown, high load). At the end of the trial a probe digit was presented, and participants had to report the digit that followed it in the original set (here the correct answer would be '4'). During the retention interval participants performed a Stroop-like task, categorizing names as politicians or singers while attempting to ignore distractor faces that appeared on some trials and were either congruent or incongruent with the name. (B) The BOLD signal difference between face present and face absent conditions is greater (bars) and the spatial extent of voxels where the difference reached statistical significance is larger (brain images) under high than under low working memory load, indicating more processing of distractor faces when the availability of working memory to control attention was reduced. Adapted from De Fockert et al (2001).

Lavie, 2004) that found a negative correlation between singleton interference and frontal activity in an attentional capture task. Top-down control functions mediated by frontal cortex may therefore be involved in preventing interference from irrelevant singletons; when the control exerted by frontal cortex was reduced, interference from the irrelevant stimulus increased.

As Lavie and De Fockert (2005) point out, previous studies on the role of working memory in visual search (Logan, 1978; Woodman, Vogel & Luck, 2001) failed to find any effect of working memory load on performance; the slopes of the search set-size functions did not interact with working memory load. Also, in a recent neuroimaging study high working memory load also did not enhance neural responses to irrelevant place images presented in the background (Yi et al, 2004). Importantly, however, unlike those studies, which involved ordinary search items and ignored background pictures, the attentional capture experiments described here examined the effect of working memory load when the ignored item was an irrelevant but highly salient singleton distractor. This suggests that the cognitive control of perceptual biases exerted by working memory is only needed in situations where preferences must be maintained despite the presence of strong competition from distractors.

1.4 Load theory and visual awareness

1.4.1 Do the effects of load tell us anything about awareness?

A large number of studies, using both behavioural and neuroimaging methods, has provided empirical support for load theory. However, in most of these studies the predictions derived from load theory have not explicitly distinguished between awareness and perceptual processing (which may not necessarily be conscious; e.g., Driver & Mattingley, 1998; Marshall & Halligan, 1988; Rees & Frith, 1997; Rees et al, 2000). Indeed, these studies (with two exceptions, see below) have used indirect measures of perceptual processing (such as reaction times and neural activity) to make inferences about attention. For example, the effects of irrelevant distractors on target RTs in response competition flanker tasks (Lavie, 1995; Lavie & Cox, 1997) are modulated by both perceptual load (which decreases distractor interference) and working memory load (which increases it). Similarly, functional neuroimaging studies have demonstrated that visual cortex activity related to task-irrelevant stimuli is reduced or even eliminated under high perceptual load in the attended task (e.g., Rees et al, 1997; Schwartz et al, 2005) but increases under high working memory load (De Fockert et al, 2001).

However, neither brain activity nor RT effects can, in themselves, provide direct evidence regarding the way conscious perception is modulated by load. RT effects convincingly demonstrate that various types of load can determine the degree of behavioural interference from distractors (and by implication, how effectively these distractors were processed), and neural measures show that

brain activity correlated with perceptual processing is modulated by load. But neither measure allows for any direct conclusions regarding awareness – whether conscious perception, the ability to report the occurrence of a stimulus, is affected by load. It is possible that the perceptual processing indicated by these measures has nothing to do with awareness. For example, it could be that distractors are never perceived consciously, and RT effects obtained with both types of load manipulation reflect unconscious processing influences on stimulus-response associations. On the other hand, it is possible that distractors are always consciously perceived, and RT effects merely reflect processes related to response selection and production. By the same token, it is also possible that neural activity reflects perceptual processes that correlate with awareness, but occur independently.

1.4.2 Preliminary evidence for the role of load in awareness

Promising preliminary evidence for the role of perceptual load in awareness comes from one of the neuroimaging studies described above (Rees et al, 1997, in which activity related to an irrelevant motion stimulus in the motion-sensitive area MT+/V5 was attenuated under high perceptual load). Rees et al (1997) also measured the duration of the motion after effect caused by the irrelevant motion stimulus, and found that participants reported a significantly shorter duration under high (compared to low) perceptual load. Since participants reported their subjective experience of motion, these results indicate that conscious visual awareness may indeed be modulated by perceptual load. However, though the motion after effect can be considered a measure of awareness, in this case it was

assessed after the load manipulation had been terminated. Any direct conclusions regarding the conscious perception of the (real) motion stimulus during performance of the task are therefore precluded.

A different study (Cartwright-Finch & Lavie, 2006) has recently attempted to assess awareness of a task-irrelevant stimulus, and its modulation by perceptual load, using an inattentional blindness paradigm. Awareness of an unexpected, task-irrelevant stimulus presented on the critical trial was found to be significantly reduced for participants who performed a high perceptual load task, compared to those who performed a low load task.

However, it has been argued that inattentional blindness does not necessarily reflect a lack of visual awareness. In inattentional blindness paradigms, awareness of the unexpected, irrelevant stimulus is assessed after the response to the task. It is therefore possible that the effect of perceptual load on inattentional blindness does not reflect reduced awareness, but reduced encoding of the unexpected stimulus into memory[1] ('inattentional amnesia'; Wolfe, 1999). The fact that both the presence and appearance of the extra stimulus are unexpected may cause the stimulus to be perceived, but to generate a weak trace that is forgotten by the time of the surprising and delayed retrospective assessment (Barber & Folkard, 1972; Bashinski & Bacharach, 1980; Davies, Kramer & Graham, 1983; Teichner & Krebs, 1974). Inattentional blindness could therefore be limited to unexpected stimuli (for example, one could claim that attention is critical for weakly encoded, unexpected stimuli to be remembered), and may teach us very little about awareness in general.

[1] As discussed earlier, this point is less convincing in the case of long-duration salient stimuli, such as a gorilla walking across the screen (Simons & Chabris, 1999).

Furthermore, if the terms of signal detection theory are applied to inattentional blindness, a limitation of this phenomenon as an experimental paradigm becomes apparent: Only reports of whether the critical stimulus was seen (hits) or not (misses) can be collected. Presentation of the critical stimulus precludes the occurrence of false alarms and correct rejections, making it impossible to assess visual sensitivity independently of response criterion. For example, it is possible that participants in the high load conditions of Cartwright-Finch and Lavie (2006) adopted a more stringent criterion than the low-load participants did for reporting the critical stimulus. The effect of perceptual load may therefore have been due to a criterion shift, rather than a true change in visual sensitivity.

1.5 General methodological approach and overview

In this thesis I investigate whether the predictions of load theory extend to visual awareness. If they do, then conscious awareness should depend on the level and type of load involved in the task performed. To examine whether this is the case, it is necessary to directly assess awareness of stimuli while manipulating load in a concurrent task, using paradigms that avoid the above criticisms.

This can be accomplished by manipulating perceptual load with regard to one set of stimuli, and measuring awareness of other stimuli that (unlike in previous research) are fully expected and presented repeatedly. In Chapter 2 I establish the role of perceptual load in the conscious detection of stimuli. In a series of

experiments, I investigate whether performing a task under high perceptual load makes observers less aware than they are under low load of the very presence of other stimuli, even though these stimuli are fully expected and serve as a different type of target.

In Chapter 3 I present a series of experiments focusing on whether perceptual load affects the subjective experience of a temporal visual pattern (rapid luminance flicker). These experiments are the first to ask whether perceptual load can alter temporal aspects of visual experience. It has recently been claimed that whereas attention improves the spatial resolution of vision, it impairs its temporal resolution (Yeshurun & Levy, 2003; Yeshurun, 2004). As load theory does not make such a distinction, it seemed particularly important to test whether the predictions of load theory generalize to awareness in the temporal domain.

In Chapter 4 I present a functional Magnetic Resonance Imaging (fMRI) study investigating the neural correlates of temporal visual awareness. Previous neuroimaging studies and the results of Chapters 2 and 3 implicate attentional mechanisms in perceptual awareness, leading to the prediction that frontal and parietal regions of cortex will be involved in the conscious perception of flicker.

The effects of working memory load on conscious awareness have not been examined as yet. In Chapter 5 I examine whether higher cognitive control functions play a role in the selection of visual stimuli for awareness. A striking phenomenon in which stimuli compete for awareness is binocular rivalry, the alternating pattern of dominance in awareness that transpires when the eyes are presented with different images (e.g., Blake & Logothetis, 2002). If working memory acts as a top-down control function when there is competition over awareness and a need to bias perception by suppressing salient stimuli, then

loading working memory should have an effect on the competition in binocular rivalry, reducing the visual system's ability to maintain a stable and coherent percept.

Finally, Chapter 6 examines the causal role of right parietal cortex in the top down control of binocular rivalry. Activity in right-lateralized frontal and parietal cortex has previously been associated with perceptual transitions in rivalry (Lumer, Friston & Rees, 1998). However, the correlational nature of neuroimaging data precludes the attribution of a causal role to activated regions. Such causal attributions can be made when using Transcranial Magnetic Stimulation (TMS), which directly interferes with brain activity (Walsh & Cowey, 2000; Walsh & Pascual-Leone, 2003). In this chapter I use TMS to establish the nature of the causal role right parietal cortex plays in the control of binocular rivalry. If this role is to induce perceptual alternations, disrupting the activity of right parietal cortex with TMS should prolong dominance durations in rivalry. Conversely, if right parietal cortex serves to maintain biases, such disruption should shorten dominance durations.

Chapter 2:

The effect of perceptual load on visual awareness

2.1 Chapter Introduction

What is the relationship between attention and perceptual awareness? Does conscious perception depend on attention to perceived stimuli? As reviewed in the General Introduction chapter, a resolution to the long standing debate between early (e.g. Broadbent, 1958; Treisman, 1960) and late (e.g. Deutsch & Deutsch, 1963; Duncan, 1980) selection views of attention has recently been proposed in the form of a load theory of selective attention and cognitive control (Lavie, 1995; Lavie & Tsal, 1994; Lavie, 2000; Lavie et al, 2004).

According to early selection views, the capacity of perception is limited; therefore, what will be perceived depends on how attention is allocated. According to late selection views, the capacity of perception is unlimited and it proceeds automatically on all stimuli, independent of attention. Since there is a great deal of empirical research supporting each of these views, as recently as the 1990s it was suggested that the early/late selection debate may never be resolved (e.g. Allport, 1993). Load theory, however, combines aspects of both views to determine whether stimuli will be perceived or not. Like the early selection view, load theory acknowledges that perception does indeed have limited capacity; but like the late selection view, it proposes that perception proceeds automatically on all stimuli it is exposed to until (and this is where the theory departs from the late selection view) capacity is consumed. The level of perceptual load in a task, therefore, dictates whether the outcome will conform to the early or late selection view: Tasks with high perceptual load will exhaust capacity in processing task-relevant stimuli, leading to task-irrelevant stimuli not being perceived (as in early selection). On the other hand, tasks with low perceptual load will not fully

consume capacity, and the left-over capacity will inevitably lead to perception of task-irrelevant stimuli (as in late selection).

The above prediction has received support from a large variety of behavioural and neuroimaging studies (see **Section 1.3.2** for a detailed review). However, most of those studies used indirect measures of irrelevant-stimulus processing (e.g., RTs in flanker tasks or neural activity related to irrelevant stimuli) rather than direct (conscious) reports to assess the effects of perceptual load. As I argued in the General Introduction (**Section 1.4.1**), while RT effects and neural measures do provide compelling evidence regarding the effects of perceptual load on visual *processing*, they cannot provide conclusive evidence regarding visual *awareness*. It is logically possible that such measures solely reflect effects on conscious processes of response selection, or conversely, on unconscious stimulus-response associations; and it has been shown that perceptual processing can occur, and lead to both behavioural and neural effects, in the absence of awareness (e.g. in priming tasks, Dehaene et al, 1998; and in pathologies such as unilateral neglect, Marshall & Halligan, 1988; Rees et al, 2000).

To test whether increasing perceptual load affects visual awareness, awareness of stimuli must be assessed directly while manipulating perceptual load in a concurrent task. One study (Cartwright-Finch & Lavie, 2006) has recently done so using an inattentional blindness paradigm. However, it is difficult to interpret the reduced awareness of an unexpected, task-irrelevant stimulus, found in that study under high load: This effect may reflect reduced encoding of the unexpected stimulus into memory rather than a true loss of awareness. Furthermore, it was not possible to distinguish changes of visual

sensitivity from shifts of response criterion within the paradigm used by Cartwright-Finch and Lavie (2006).

The purpose of the present study was therefore to directly investigate the effect of perceptual load on visual awareness, using a paradigm that would avoid the criticisms detailed above. Participants simultaneously monitored for the appearance of two types of target – one at fixation (central targets), the other in the periphery (peripheral targets). Perceptual load was manipulated for central targets.

Unlike in inattentional blindness, peripheral stimuli were both relevant and fully expected (participants knew that they would appear and what they would look like). Moreover, the paradigm entailed continuous monitoring over an extended duration, with the two types of target appearing only occasionally and never presented at the same time. As responses to both types of target were given as soon as they were perceived, rapid forgetting or interference from producing responses to a concurrent target cannot account for any effect of perceptual load found.

It has been suggested (Duncan, 1980) that when a single target is present in the display, there will be little or no performance decrement due to divided attention, and that for divided attention costs to arise it is necessary for targets to appear simultaneously and require independent identification and a separate response. However, in this paradigm the non-simultaneous presentation of the two types of target rules out any account of perceptual load effects in terms of such a two-target cost.

Finally, the paradigm used allowed for responses from each participant to be collected for a large number of trials under different load conditions, enabling a

within-subject assessment of visual awareness using an objective measure of reported visual sensitivity, d' (Macmillan & Creelman, 1991).

Load theory predicts that the depletion of capacity under high load for central targets will lead to lower levels of attention being deployed to peripheral locations, resulting in reduced awareness of peripheral targets, even when they are not concurrent with central targets. This direct implication of load theory to visual awareness has not been tested before.

2.2 Experiment 1

2.2.1 Introduction

To assess the effect of perceptual load on visual awareness, a paradigm requiring participants to concurrently monitor different locations and detect two types of target was used. The load manipulation was applied to the targets presented at fixation (central targets): For identical stimuli (a rapid succession of crosses) participants performed either a low-load feature search (responding to the occasional appearance of red crosses among other colours), or a high-load conjunction search (responding to upright yellow and inverted green crosses). This is a well-established manipulation of perceptual load, shown to be effective in both behavioural studies (where RTs increased and accuracy declined under high load, e.g., Lavie, 1995; Triesman, 1988) and neuroimaging studies (where parietal activity increased under high load, Wojciulik & Kanwisher, 1999). This task has also been previously shown to modulate brain activity in response to

irrelevant stimuli in peripheral locations in retinotopic visual cortex (Schwartz et al, 2005).

Simultaneously, participants also continuously monitored two pre-defined locations (situated diagonally from each other at equal distances from fixation and marked by place-holder squares) while ignoring two other locations (situated on the other diagonal), for the occasional appearance of a small, meaningless grey shape (the peripheral target). If perceptual load consumes capacity that is required for awareness, then high (compared to low) perceptual load at fixation should lead to lower detection sensitivity to peripheral targets.

2.2.2 Method

Participants: Twelve volunteers participated in the experiment. All had normal or corrected-to-normal vision. One participant could not reliably identify the peripheral stimulus (<30% hits) and was therefore excluded from the analysis. The remaining eleven participants had a mean age of 27.4 (range 18-35). Four were female and eight right-handed.

Stimuli and apparatus: Participants sat in a dark room, viewing an 18'' screen (Mitsubishi Diamond Pro 920, resolution 640*480, 60 Hz refresh rate) from a distance of 57 cm. Head position was stabilized by a chin rest. Stimuli were created and presented using Matlab on a Dell PWS650 computer.

Visual stimuli were presented on a black background, and included (**Figure 2.1**) centrally-presented crosses, spanning 0.7° (vertical line) by 0.4° (horizontal line). Crosses could appear in any of six colours (red, green, yellow, blue, cyan,

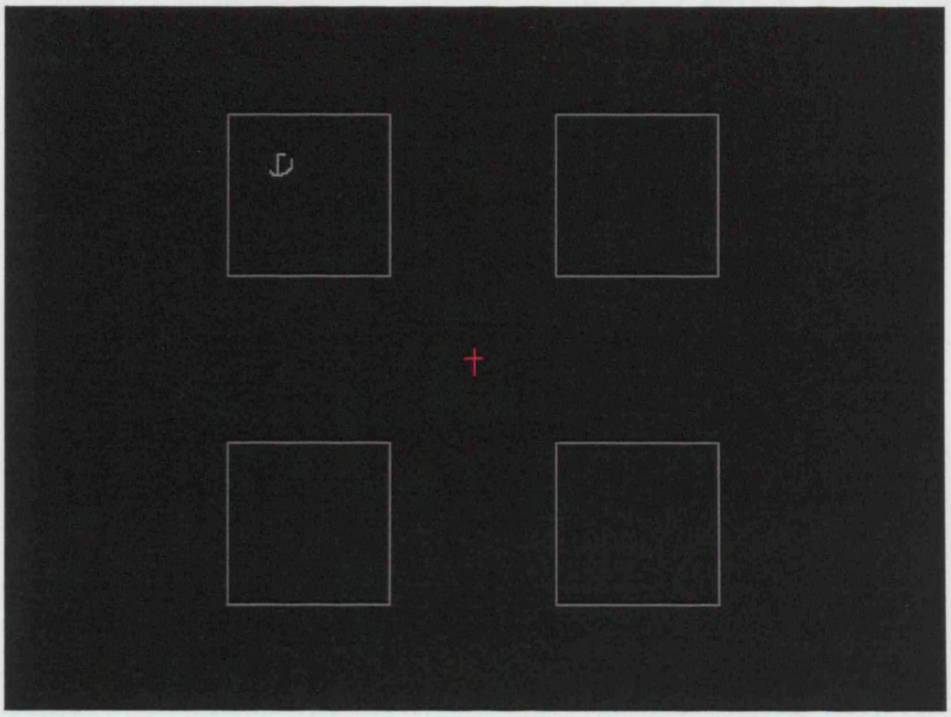

Figure 2.1. Experiment 1: The visual stimuli in a trial. The purple upright cross is a non-target central stimulus. Central targets (red crosses in either orientation under low load; upright yellow and inverted green crosses under high load) were defined at the beginning of each trial. A grey meaningless shape, which served as the peripheral stimulus, appears in the top left place-holder square. For display purposes, the peripheral stimulus shown is brighter than the one used in the actual experiment. Peripheral stimuli appeared in random locations within any of the four squares. The two attended squares in each trial were indicated by a diagonal line appearing at the beginning of the trial. This image only shows the central portion of the screen, the rest of which was a uniform black.

and purple) and two orientations (upright or inverted; the horizontal line of the cross was placed either one pixel above or below the centre of the vertical line). In addition, four grey place-holder squares (3.8° by 3.8°), arranged at the vertices of an imaginary square centred on fixation and at an eccentricity of 5.3° (distance from the squares' centre to fixation) were presented continuously throughout the trial. A small (0.6° * 0.6°), grey (RGB values: 15, 15, 15) meaningless shape

which served as the peripheral stimulus could appear anywhere within the four place-holder squares. During inter-trial intervals, a small grey dot appeared at fixation. Instructions preceding the next trial were given in white text which indicated the target crosses for the next trial ('Red crosses' or 'Upright yellow / inverted green'). On experimental trials (see below), a diagonal line appearing below fixation indicated the attended diagonal for the next trial. On control trials the word 'ONLY' appeared instead of the diagonal line.

Design: Participants attended to a rapid succession of crosses presented at fixation (central stimuli; **Figure 2.2**). Perceptual load was manipulated so that for identical stimulus parameters, participants performed either a low-load feature search (responding to red crosses among other cross colours), or a high-load conjunction search (responding to upright yellow and inverted green crosses). Concurrently, participants were required to detect the occasional appearance of a small, meaningless grey shape (the peripheral stimulus) in two of four peripheral locations marked by squares (attended locations were always positioned diagonally to each other), while ignoring the shape when it appeared in unattended locations. Target crosses are henceforth referred to as central targets, and presentations of the peripheral stimulus in the attended diagonal are referred to as peripheral targets. Central targets and peripheral stimuli never appeared simultaneously. On experimental trials participants monitored for the appearance of both central and peripheral targets. Control trials, in which participants only monitored for central targets, were also included to verify that the load manipulation was effective regardless of extra task requirements.

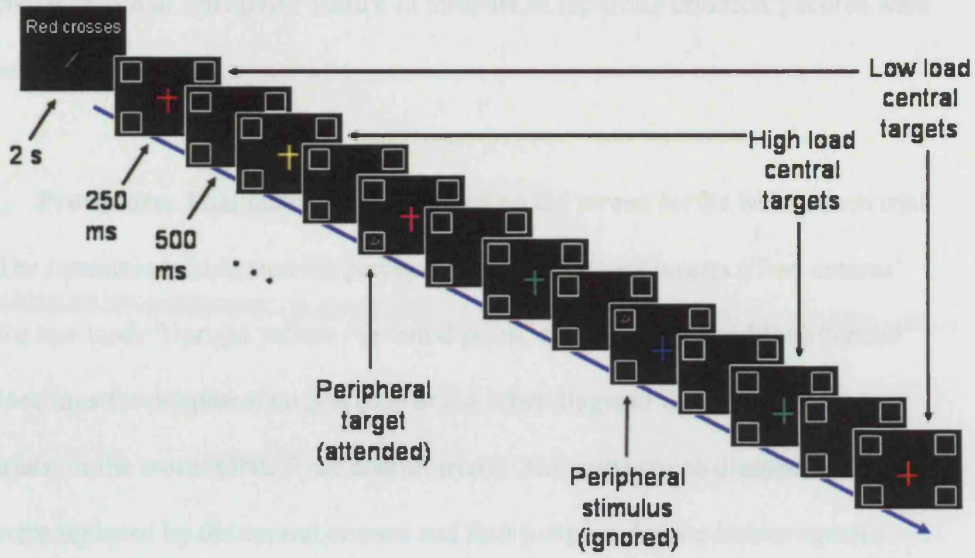

Figure 2.2. Experiment 1: The sequence of events during a trial. At the beginning of each trial, a written instruction defined the central targets for that trial. Here red crosses were designated as central targets, making this a low perceptual load trial. A diagonal line indicated the two attended squares for peripheral target detection (the word 'ONLY' replaced the line on control trials). Here the top right and bottom left squares were attended. The instructions were displayed for 2 s. Subsequent stimulus presentation consisted of a series of central stimuli appearing for 250 ms each with a stimulus onset asynchrony (SOA) of 750 ms; peripheral place-holder squares which were presented constantly; and peripheral stimuli appearing occasionally at random locations within the squares. Note that the stimulus sequence parameters were identical under all conditions. Indicated are central stimuli serving as targets under low and high perceptual load. Also indicated are target and non-target peripheral stimuli. Image not to scale.

For central targets, a 2 (load: Low, high) by 2 (experimental or control trial) factorial design was therefore employed. Participants were only required to detect peripheral targets on experimental trials. Performance measures were recorded separately for low and high perceptual load. RTs and accuracy rates were measured for central targets in both experimental and control trials. For peripheral targets, detection (hit) and false alarm rates, as well as d' (a criterion-

free measure of sensitivity[1]) and c (a measure of reporting criterion[2]) scores were recorded.

Procedure: Trial instructions appeared on the screen for 2 s before each trial. The instructions indicated the perceptual load for central targets ('Red crosses' for low load; 'Upright yellow / inverted green' for high load), and the attended locations for peripheral targets (one or the other diagonal line on experimental trials, or the word 'ONLY' on control trials). The instructions disappeared and were replaced by the central crosses and four peripheral place-holder squares (see **Figure 2.2** for a schematic diagram of trial sequence). Each cross was displayed for 250 ms, followed by a blank period of 500 ms before the appearance of the next cross. Participants were instructed to press a keyboard key (the left arrow) with their right index finger as quickly as possible whenever a central target appeared. Responses were recorded as correct if they were made within a response window of 1500 ms following central target onset. Cross order (colour and orientation) was randomized, with the constraint that two target crosses could not appear on successive presentations (to avoid overlap of response windows). Each trial lasted 39.75 s, during which 53 crosses were presented. Of these, four (7.5%) were target crosses (two upright and two inverted red crosses under low load; two upright yellow and two inverted green crosses under high load).

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[1] This measure was calculated using the formula $d' = Z(H) - Z(F)$, where Z(H) stands for the Z-score associated with the probability of a Hit, and Z(F) for that associated with the probability of a False alarm (Macmillan & Creelman, 1991).

[2] This measure was calculated using the formula $c = -0.5[Z(H) + Z(F)]$ (Macmillan & Creelman, 1991).

The place-holder squares were constantly present throughout the trial. At random times (but not within the first 2.5 s of a trial, to allow participants to become engaged in the central target search), the grey shape serving as peripheral stimulus appeared in a random location within one of the squares. Peripheral stimuli appeared for 250 ms, always simultaneously with a central stimulus. Importantly, peripheral stimuli never appeared at the same time as a central target. Participants were instructed to press a keyboard key (the left alt) with their left index finger whenever they detected a peripheral target (a peripheral stimulus presented in an attended location). Responses were recorded as correct if they were made within a response window of 2000 ms following peripheral target onset. To avoid an overlap of response windows, peripheral stimuli could not appear within 2000 ms of a previous peripheral stimulus (regardless of whether it was a target or not). To avoid any priming effects, peripheral stimuli could also not appear in the same location within less than 7 s of the previous presentation. On each trial, around 9-12 stimuli were presented in peripheral locations. On average, half of them were peripheral targets (appearing in the attended diagonal).

An inter-trial interval of 5 s followed each 39.75 s trial. During this period a grey central fixation dot appeared on the screen. This was followed by the instructions for the next trial. Each block comprised six trials, one trial of each type (2 load conditions by 3 possible instructions regarding peripheral targets: Attend to one or the other diagonal on experimental trials, or the word 'only' for control trials in which only central targets were to be detected). The experiment consisted of six blocks, with a participant-terminated break between blocks. Trials of the same type could not occur in the same place in different blocks, and

perceptual load within a block alternated between low and high. The load of the first trial in a block alternated between blocks. The load of the first trial in the first block was counterbalanced across participants.

At the beginning of the experimental session, each participant was shown an image of the peripheral stimulus. Participants then performed one practice block in which the peripheral stimulus was brighter than it would be in the actual experiment (RGB values: 26, 26, 26), and another practice block in which the peripheral stimulus was the same as that used in the experiment. The order of trials in the practice blocks was the same as in the first block of the experiment.

2.2.3 Results and discussion

Central target detection: To verify that the perceptual load manipulation was effective, RTs and accuracy rates for central target detection were entered into 2 (Load: Low, high) by 2 (trial type: experimental, control) repeated-measures ANOVAs. For RTs, the analysis revealed a main effect of load ($F_{(1,10)}$ = 157.36, $\underline{MSE}$ = 1747.04, $p < 0.001$) and a main effect of trial type ($F_{(1,10)}$ = 19.63, $\underline{MSE}$ = 1340.34; $p = 0.001$), but no interaction ($F_{(1,10)}$ = 2.33, $\underline{MSE}$ = 489.51, *ns*; see **Table 2.1**).

For accuracy rates (the percentage of detected central targets), the analysis again revealed a main effect of load ($F_{(1,10)}$ = 22.91, $\underline{MSE} = 9.9*10^{-3}$, $p = 0.001$) and a main effect of trial type ($F_{(1,10)}$ = 8.83, $\underline{MSE} = 4.35*10^{-3}$; $p = 0.014$), but no interaction ($F < 1$, *ns*; see **Table 2.2**).

For both measures, the main effects are easy to interpret: RTs were slower and accuracy rates lower under high (compared to low) perceptual load.

Table 2.1. Experiment 1: Mean RTs for central target detection, in ms (numbers in parentheses represent 1 standard error of the mean)

	Perceptual load		Effect of load
	Low	High	(high – low)
Control trials	534 (21)	682 (20)	148
Experimental trials	573 (23)	741 (21)	168

Similarly, Reaction times were slower and accuracy rates lower in experimental (compared to control) trials. This indicates a performance cost associated with higher perceptual load, as well as with the extra requirements of peripheral target detection. Importantly, the absence of an interaction indicates that the cost incurred by adding the peripheral detection did not significantly modulate the effect of perceptual load. Hence, the load manipulation can be considered reliable regardless of whether it is being performed on its own or concurrently with detection of unrelated targets. Therefore, the next experiments did not include control trials.

Table 2.2. Experiment 1: Mean accuracy rates for central target detection, in percentages (numbers in parentheses represent 1 standard error of the mean)

	Perceptual load		Effect of load
	Low	High	(low – high)
Control trials	98.2 (1)	85.8 (4)	12.4
Experimental trials	94.3 (2)	77.9 (4)	16.4

Peripheral target detection: The mean d' scores, mean percentages of hits and false alarms and c (criterion) scores for peripheral target detection, as a function of perceptual load, are presented in **Table 2.3**. In order to assess sensitivity while taking both detection and false alarm rates into account, criterion-free d' scores were calculated for each participant under low and high perceptual load. As predicted, peripheral target detection was affected by perceptual load at fixation. d' scores were reduced under high load compared to low load, $t_{(10)} = 3.169$, SEM = 0.13, $p = 0.01$ (two-tailed). Visual sensitivity in the periphery was therefore impaired by high perceptual load at fixation. The constituent measures of the d'-score were similarly affected: Detection rates (hits) were lower under high load compared to low load, and participants made more false alarms under high load than under low load, though these trends only reached significance using one-tailed tests (hits: $t_{(10)} = 1.869$, SEM = 0.016, $p = 0.046$; false alarms: $t_{(10)} = 2.08$, SEM = 0.0013, $p = 0.032$). It should be noted that across all participants and conditions, only a single false alarm could have been due to a failure to respond within the specified response window for

Table 2.3. Experiment 1: Mean percentages of hits and false alarms and mean d' and c scores for peripheral target detection as a function of perceptual load at fixation (numbers in parentheses represent 1 standard error of the mean)

Perceptual load	Hit rate (%)	FA rate (%)	d'	c
Low	87.6 (2.6)	0.09 (0.04)	4.35 (0.12)	0.93 (0.07)
High	84.5 (2.9)	0.34 (0.1)	3.93 (0.14)	0.87 (0.09)

FA = false alarm

peripheral targets (as it was given more than 2000 ms after an undetected peripheral target). Finally, a paired-sample t-test revealed no effect of perceptual load on the criterion-measure c ($t_{(10)} = 0.7$, SEM = 0.08, *ns*). The effect of load on hit rates, therefore, cannot be attributed to a criterion shift (e.g., participants adopting a more stringent criterion for reporting peripheral targets under high load).

Importantly, the effects described above occurred despite peripheral targets never occurring simultaneously with a central target. These effects cannot, therefore, be attributed to a two-target cost (e.g., Duncan, 1980). The effect of central-target perceptual load on peripheral target detection can also not be attributed to a form of 'attentional blink' (Shapiro, Arnell, & Raymond, 1997). Here, peripheral targets could only appear a minimum of 750 ms after the onset of a central target (and on average they were presented over 2 s from the onset of the last central target), whereas the attentional blink subsides completely by 500 ms after the onset of the first target (Shapiro et al, 1997).

However, a different issue may have had led to an artefactual inflation of d' scores under both load conditions. This issue was addressed in Experiment 2.

2.3 Experiment 2

2.3.1 Introduction

The results of Experiment 1 showed that increasing perceptual load for central targets caused a reduction in visual sensitivity to peripheral targets.

Participants became less aware of peripheral targets when central target detection exhausted their attentional resources. However, it should be noted that for both high and low perceptual load, the sensitivity measure d' was very high (3.93 and 4.35 for high and low load, respectively). Peripheral target detection was thus nearly optimal under both conditions (a d' score of 4.65 conforms to 99% detection and 1% false alarms, and is often considered the effective ceiling for sensitivity measurement; Macmillan & Creelman, 1991). For such extreme results, very small differences in detection or false alarm rates can make a big difference to the final d' score. Importantly, the d' score takes into account the probability of false alarms (i.e. the number of false alarms as a fraction of the number of opportunities for a false alarm). As described above, the number of false alarms was greater under high perceptual load. However, as there were no specific, designated times during trials when participants were required to decide whether or not a peripheral target had appeared, calculating the *probability* of false alarms entailed dividing the number of false alarms by the total number of non-target central-stimulus presentations. This led to extremely small probability values (see **Table 2.3**), which may have artificially inflated d' scores under both high and low perceptual load. As at extreme values, small differences in false alarm rates can make a big difference to d' scores, it is possible that the magnitude (though not the direction) of the effect of load at fixation on peripheral target detection in Experiment 1 was exaggerated.

The aim of Experiment 2 was to address these issues by making peripheral target detection more challenging, as well as constraining the opportunities (and therefore the probabilities) for both hits and false alarms when detecting peripheral targets. Presentations of the peripheral target were again time-locked

to the onset of a central stimulus, but were shorter than in Experiment 1, and were followed by a mask appearing over all four peripheral place-holder squares. In addition, masks would occasionally appear without a peripheral stimulus preceding them. Thus, the probability of hits could be calculated as the proportion of detected peripheral targets out of all target + mask presentations, and the probability of false alarms could be calculated as the proportion of responses to masks (not preceded by peripheral targets) out of all presentations of such masks. The number of mask presentations was much smaller than the number of non-target central stimulus presentations (which served as the basis for the calculation of false alarm probability in Experiment 1). Therefore, sensitivity measures obtained in Experiment 2 should not be inflated by artificially low false-alarm probabilities. This should lead to more realistic d' measures than in Experiment 1, under both high and low perceptual loads. If the effect of load on visual sensitivity found in Experiment 1 was not exaggerated due to extreme probability values, the effect should be replicated, with similar magnitude, in Experiment 2.

2.3.2 Method

Participants: Ten new volunteers took part in the experiment. Their mean age was 27 (range 19-39), six were female and all were right-handed. All had normal or corrected-to-normal vision.

Stimuli and apparatus: These were the same as in Experiment 1, except for the addition of a mask consisting of grey lines (RGB values: 128, 128, 128) on a

black background. The dimensions of the mask were similar to the inner dimansions of the peripheral place-holder squares. It appeared over all four squares after each peripheral stimulus and, occasionally, without a preceding peripheral stimulus (see **Figure 2.3**).

Design and procedure: These were similar to Experiment 1, except for the following differences: First, there were no control trials. Participants performed both central and peripheral target detection on all trials. In addition, masks (**Figure 2.3**) appeared after each peripheral target, after each peripheral non-target (peripheral stimulus in the unattended diagonal) and occasionally without

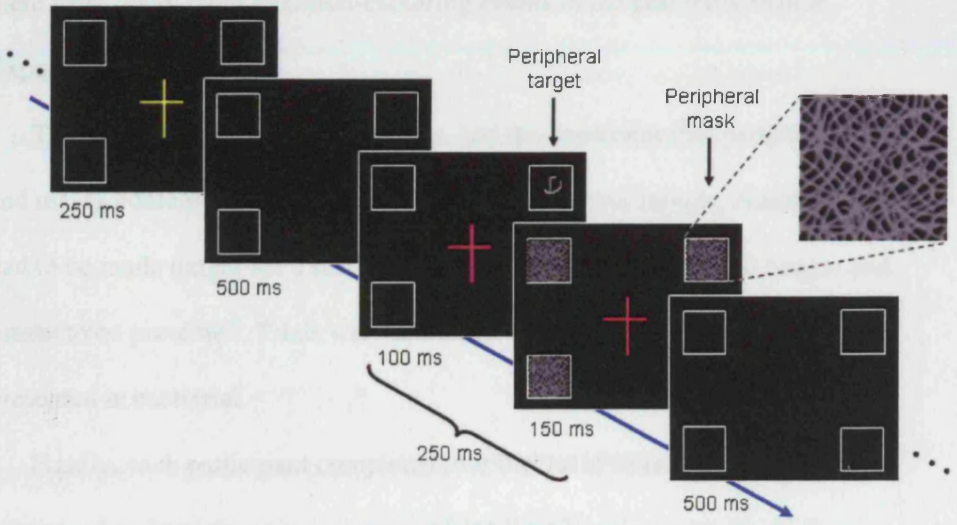

Figure 2.3. Experiment 2: Sequence of stimuli with masks. The sequence during trials was similar to that of Experiment 1, except that peripheral stimuli were only shown for the 100 of the 250 ms of central stimulus presentation. During the remaining 150 ms, a mask (shown enlarged, top right) was presented over all four peripheral squares. When masks were presented without a preceding peripheral stimulus, they appeared during the last 150 ms of central stimulus presentation.

any preceding peripheral stimulus (the proportion was a third for each of these three types of mask). Like peripheral stimuli, masks could also not appear simultaneously with a central target. Peripheral stimuli were still presented simultaneously with non-target central stimuli, but were now presented during the first 100 ms of the 250 ms central-stimulus presentation. Masks were presented during the remaining 150 ms. When masks were presented on their own, they appeared during the last 150 ms of central-stimulus presentation.

Another difference was that more central targets were presented than in Experiment 1 – instead of 4, between 8 and 16 (average 12.5) central targets were presented on each trial. This was done in order to prevent a shift in prioritization towards peripheral target detection, which may have occurred as the inclusion of masks, both after peripheral non-targets and on their own, meant there were many more attention-capturing events in the periphery than in Experiment 1.

The addition of more central targets, and the constraint that peripheral targets and masks could not appear simultaneously with central targets, meant that trials had to be made longer for a sufficiently large number of peripheral targets and masks to be presented. Trials were therefore 48 s long; 64 central stimuli were presented in each trial.

Finally, each participant completed four blocks of trials. Each block comprised eight trials, arranged in an ABBABAAB order (with A and B denoting high and low perceptual load or vice-versa) to minimize order effects. Trials of the same type did not occur more than once in the same place in a block. The perceptual load of the first trial within a block alternated between blocks, and was counterbalanced across participants.

2.3.3 Results and discussion

Central target detection: As in Experiment 1, RTs under high perceptual load (M = 592 ms) were longer than under low perceptual load (M = 462 ms), $t_{(9)}$ = 12.548, SEM = 10.384 ms, $p < 0.001$. Accuracy rates were lower under high (M = 89%) than under low load (M = 94.2%), $t_{(9)} = 3.905$, SEM = 1.3%, p = 0.004. Therefore, the load manipulation was again effective.

Peripheral target detection: The mean d' scores, c scores and mean percentages of hits and false alarms for peripheral targets, as a function of perceptual load, are presented in **Table 2.4**. As in Experiment 1, perceptual load for central targets significantly affected sensitivity to peripheral targets: d' scores were lower under high than under low perceptual load; $t_{(9)} = 3.166$, SEM = 0.1235, p = 0.011. Note that the d' scores found in this experiment are much lower than those found in Experiment 1 (a difference of 1.59 for low load and 1.57 for high load). Introducing masks as a basis for calculating false-alarm probabilities (by having a similar amount of opportunities for hits and false

Table 2.4. Experiment 2: Mean percentage hits and false alarms, and mean d' and c scores for peripheral target detection as a function of perceptual load at fixation (numbers in parentheses represent 1 standard error of the mean)

Perceptual load	Hit rate (%)	FA rate (%)	d'	c
Low	69 (5.36)	1.7 (0.52)	2.75 (0.19)	0.83 (0.09)
High	62 (5.44)	2.9 (0.82)	2.36 (0.22)	0.85 (0.09)

FA = false alarm

alarms) therefore prevented inflation of d' scores. Importantly, though the d' scores were significantly lower than in Experiment 1, the magnitude of the load effect was almost identical (a difference of 0.39 here versus 0.42 in Experiment 1).

As in Experiment 1, hit rates for peripheral targets were again affected by perceptual load: They were higher under low than under high perceptual load, $t_{(9)} = 4.072$, SEM = 0.0172, p = 0.003.

Two kinds of false alarm were examined: Reports of a peripheral target following a mask preceded by a peripheral stimulus in an unattended location, and reports of a peripheral target following a mask alone. There was a non-significant trend for more false alarms under high (compared to low) load both when masks followed non-target peripheral stimuli (M = 1% versus 3% for low and high load, respectively; $t_{(9)} = 1.242$, SEM = 0.0113, *ns*), and when masks appeared without a preceding stimulus (M = 1.5% versus 2.5% for low and high load, respectively; $t_{(9)} = 1.5$, SEM = 0.0067, *ns*). As the average percentage of false alarms was the same for both types (2%), they were combined into a single measure incorporating all false alarms, which was used in the calculation of the d' score. The combined false alarm rates again showed a non-significant trend toward more false alarms under high than under low perceptual load ($t_{(9)} = 1.585$, SEM = 0.0076, *ns*; see **Table 2.4**).

Finally, a paired-sample t-test, used to see whether the effect of load on hit rates may not be partly attributed to a criterion shift (e.g., by participants adopting a more strict criterion for reporting the peripheral target under high load), revealed no effect of perceptual load on the criterion-measure c ($t_{(9)} = 0.33$, SEM = 0.07, *ns*).

The current design made it possible to examine whether the effect of perceptual load on visual sensitivity was due to the higher demands placed continuously on attentional resources under high load, or whether it was related to central target detection. It is possible, for example, that the effect found for peripheral target detection may be driven by a decline in sensitivity to peripheral targets immediately following a central target, and that this decline would be stronger under high than under low load. If this were the case, then for peripheral targets occurring after a longer time, similar performance under both loads would be expected and the overall level of performance should be higher than immediately following a central target.

To investigate this issue, d' scores were calculated under each load separately for peripheral presentations occurring during the first stimulus presentation following a central target ('near' presentations), and during presentations occurring more than one stimulus after the last central target ('far' presentations). An examination of the data reveals no effects of target-proximity: Performance was worst under high load in the 'far' condition ($\underline{M}$ = 2.38) and slightly better under high load in the 'near' condition ($\underline{M}$ = 2.4). Performance under low load was better, not worse, in the 'near' than in the 'far' condition ($\underline{M}$ = 3.03 and 2.58 for the 'near' and 'far' conditions, respectively). Indeed, when the d' scores were entered into a 2 (load: Low or high) by 2 (proximity to the last central target: 'near' or 'far') repeated measures ANOVA, a main effect of load was found ($F_{(1,9)} = 11.913$, $\underline{MSE} = 0.14$; $p = 0.007$), but there was no significant effect of proximity to the last target ($F_{(1,9)} = 2.544$, $\underline{MSE} = 0.22$, *ns*) and no interaction ($F_{(1,9)} = 2.756$, $\underline{MSE} = 0.177$, *ns*). Rather than a target-related cost, this pattern of results is consistent with a view of high perceptual load at fixation as

continuously exhausting attentional resources to a greater degree than low load, leading to a lower level of attentional deployment to the periphery.

2.4 Experiment 3

2.4.1 Introduction

In Experiments 1 and 2, peripheral target detection involved attending to two locations while ignoring two others. This raises the question of whether the effect of perceptual load for central targets on visual sensitivity to peripheral targets is indeed due to reduced attentional capacity under high perceptual load, or whether it depends on the need to inhibit input from irrelevant locations. If the former option is correct, then the effect of load should occur even when all peripheral locations are attended. This possibility was investigated in Experiment 3, in which there were no ignored locations – all four peripheral locations were designated as target locations. If the effect of perceptual load on peripheral visual sensitivity depends on the need to coordinate attending to relevant stimuli while inhibiting irrelevant ones, then this effect should now disappear. If, on the other hand, the effect is indeed due to a reduction in attentional capacity, it should be found again in this experiment.

2.4.2 Method

Participants: Ten new volunteers participated in the experiment. Their mean age was 22.9 (range 19-39), four were female and eight were right-handed. All had normal or corrected-to-normal vision.

Stimuli, design and procedure: The visual stimuli used in the experiment were identical to those of Experiment 2, except that no diagonal lines appeared in the trials' instructions. The design and procedure were similar to those of Experiment 2, except for the following differences: All four peripheral locations were now used as peripheral target locations, and no locations were to be ignored during trials. Peripheral target + mask and mask-only presentations therefore appeared with equal probability. To allow for more peripheral targets to be presented, the minimal time between peripheral targets in the same location was shortened from 7 to 5 s.

2.4.3 Results and discussion

Central target detection: As in the previous two experiments, the perceptual load manipulation for central targets was effective. Participants' RTs were longer under high load ($\underline{M}$ = 568 ms) than under low load ($\underline{M}$ = 441 ms), $t_{(9)} = 11.602$, $\underline{SEM}$ = 11.01, $p < 0.001$; and their accuracy levels were lower under high load ($\underline{M}$ = 92%) than under low load ($\underline{M}$ = 97.8%), $t_{(9)} = 3.914$, $\underline{SEM}$ = 1.48%, $p = 0.004$.

Peripheral target detection: The mean d' and c scores, and mean percentages of hits and false alarms for peripheral targets, as a function of perceptual load, are presented in **Table 2.5**. There was a significant effect of perceptual load on the sensitivity measure, d' ($t_{(9)} = 2.57$, SEM = 0.14, $p = 0.03$). High perceptual load at fixation therefore reduced visual sensitivity in the periphery even when there was no need to coordinate attention to some locations with inhibition of others. Hit rates were lower under high than under low perceptual load, but this difference only approached significance in a one-tailed t-test ($t_{(9)} = 1.802$, SEM = 2.55%, $p = 0.052$, one-tailed). Similarly false alarm rates were higher under high (compared to low) load, a difference which again only approached one-tailed significance ($t_{(9)} = 1.616$, SEM = 0.37%, $p = 0.07$, one-tailed). As in the previous experiments, the criterion measure c did not differ significantly between low and high load ($t_{(9)} = 0.48$, SEM = 0.07, *ns*).

As in Experiment 2, an examination of sensitivity to peripheral targets occurring either immediately after a central target ('near'; mean d' scores: 3 and 2.49 for low and high load, respectively) or after a longer period ('far'; mean d' scores: 2.86 and 2.67 for low and high load, respectively) revealed that the effect

Table 2.5. Experiment 3: Mean percentage hits and false alarms and mean d' and c scores for peripheral target detection as a function of perceptual load at fixation (numbers in parentheses represent 1 standard error of the mean)

Perceptual load	Hit rate (%)	FA rate (%)	d'	c
Low	70.5 (5.9)	1 (0.26)	3.03 (0.25)	0.85 (0.09)
High	65.9 (5)	1.6 (0.4)	2.67 (0.2)	0.89 (0.07)

FA = false alarm

of perceptual load is not driven by a decline in performance under high load immediately following a central target. A 2 (load: Low or high) by 2 (proximity to last target: 'near' of 'far') repeated-measures ANOVA revealed a main effect of load ($F_{(1,9)} = 8.536$, $\underline{MSE} = 0.14$, $p = 0.017$), but no effect of proximity to the last target ($F_{(1,9)} < 1$, *ns*) and no interaction ($F_{(1,9)} = 1.449$, $\underline{MSE} = 0.167$, *ns*).

The results of Experiment 3 rule out the possibility that the effect of perceptual load at fixation on visual sensitivity to peripheral targets depends on the requirement to coordinate attention to certain peripheral locations while ignoring others. Rather, it is consistent with the proposition that when attentional resources are consumed by high perceptual load at fixation, lower levels of attention are deployed to peripheral locations, resulting in lower sensitivity, and therefore reduced awareness of stimuli, in those locations.

The results of Experiments 1 to 3 have established that perceptual load at fixation reduces visual sensitivity in the periphery. Furthermore, this effect does not require simultaneous presentation of peripheral targets and central ones – attending to central stimuli continuously, rather than the actual detection of central targets (c.f. Duncan, 1980), is what causes the effect of load on peripheral sensitivity.

2.5 Experiment 4

2.5.1 Introduction

In Experiments 1 to 3, high perceptual load at fixation reduced visual sensitivity in the periphery, implying a reduction in the deployment of attention to the periphery under high load. However, peripheral targets were always presented simultaneously with a central stimulus (albeit not a target). It is therefore possible that the presence of central stimuli, which competed with peripheral targets for processing (Desimone and Duncan, 1995), was in itself sufficient to reduce sensitivity to peripheral targets, and that this effect was exacerbated under high perceptual load. Load theory does not stipulate that the presence of a competing stimulus is necessary for load effects to occur, though. In order to assert that the depletion of attentional resources under high load causes the effect, it is necessary to demonstrate that the reduction in peripheral visual sensitivity under high perceptual load can occur independently of the simultaneous presence of a competing central stimulus.

If the effect of load is indeed due to the depletion of attentional resources during processing of central stimuli, then this effect should occur even if peripheral targets are presented on their own, during the inter-stimulus-interval of central stimuli, rather than simultaneously with a central stimulus. If, on the other hand, the effect is due to competition from simultaneously-presented central stimuli, then it should only occur during such simultaneous presentations, and not when the peripheral stimulus is presented on its own. In the present experiment, these possibilities were investigated by presenting peripheral targets

both simultaneously with central stimuli (as in Experiments 1 to 3) and during the central stimuli's inter-stimulus-interval.

2.5.2 Method

Participants: Eleven new participants took part in this experiment. Their mean age was 23.5 (range 21-30), six were female and ten were right handed. All had normal or corrected-to-normal vision.

Stimuli, design and procedure: The stimuli and procedure were identical to those of Experiment 3, except for the following changes. Peripheral targets and masks could appear either at the same time as central stimuli (as in the previous experiments; this is henceforth referred to as the simultaneous condition) or during central stimuli's inter-stimulus-interval (the non-simultaneous condition; see **Figure 2.4**). In the non-simultaneous condition, the target + mask presentation occurred in the latter 250 ms period of the central stimuli's 500 ms inter-stimulus-interval. In both the simultaneous and non-simultaneous conditions masks could be presented without a preceding peripheral target. The timing of the masks was the same (100 ms or 600 ms after central stimulus onset) regardless of whether they were preceded by a peripheral target. On each trial, around half of the peripheral targets and masks were randomly assigned to the simultaneous condition, and around half to the non-simultaneous condition.

As before, central targets could not be presented simultaneously with a peripheral target (in the simultaneous condition). In addition, the central stimulus following a peripheral target in the simultaneous condition, and the central

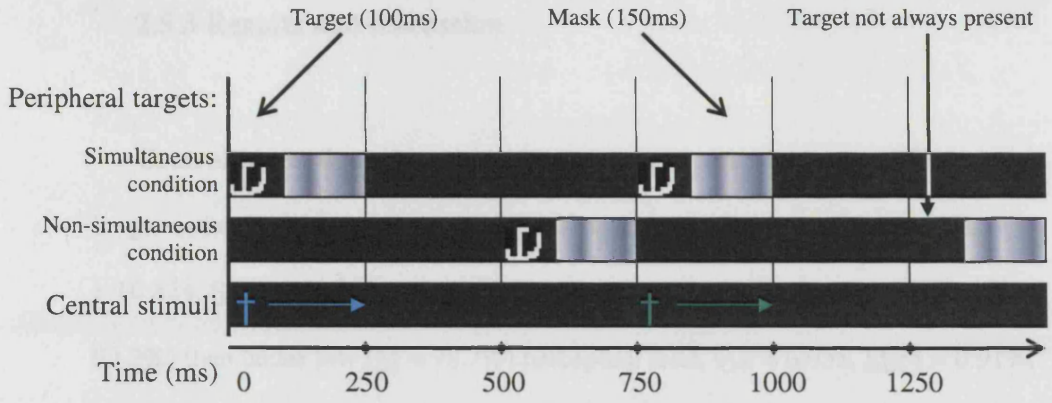

Figure 2.4. Experiment 4: Schematic timeline of the central and peripheral stimulus presentations. In the simultaneous condition (top line) the onset of the peripheral target was simultaneous with that of the central stimulus. The peripheral target was presented for 100 ms, followed by a mask presented for 150 ms. The offset of the mask was simultaneous with that of the central stimulus. In the non-simultaneous condition, the sequence was the same except the onset of the peripheral target occured 250 ms after the offset of the last central stimulus.

stimuli before and after non-simultaneous peripheral targets, could not be central targets.

The experiment therefore had a 2 (load: low, high) by 2 (peripheral target timing: simultaneous, non-simultaneous) factorial design for peripheral target detection. As there were four conditions (rather than two as in the previous experiments), each participant performed eight blocks of trials (rather than four as in Experiments 2 and 3), to ensure a sufficient amount of target presentations in each condition.

2.5.3 Results and discussion

Central target detection: As in the previous experiments, mean RTs were longer under high perceptual load (M = 576) than under low load (M = 440), $t_{(10)}$ = 10.424, SEM = 13.082, $p < 0.001$. Accuracy was lower under high (M = 93.2%) than under low (M = 98.7%) perceptual load, $t_{(10)} = 6.055$, SEM = 0.91%, $p < 0.001$.

Peripheral target detection: If the effect of perceptual load at fixation on visual sensitivity in the periphery is indeed due to lower levels of attention being continuously deployed to the periphery under high load, then this should occur for the non-simultaneous condition as well as the simultaneous one. Therefore, there should be a main effect of load on peripheral target detection, with no effect of peripheral-target timing and no interaction. If, on the other hand, the effect of load is due to competition from the central stimulus, then it should occur for the simultaneous but not the non-simultaneous condition. There should, therefore, be a main effect of timing and an interaction between timing and load (though not necessarily a main effect of load, due to the absence of an effect in the non-simultaneous condition).

The mean d' scores, mean percentages of hits and false alarms and the criterion measure c for peripheral targets as a function of perceptual load are presented in **Table 2.6**. d' scores, hit rates, false alarm rates and the criterion measure c were entered into 2 (load: low, high) by 2 (peripheral target timing: simultaneous, non-simultaneous) repeated-measures ANOVAs. For d' scores, there was a main effect of load ($F_{(1,10)} = 5.056$, MSE = $7.2*10^{-2}$, $p = 0.048$),

Table 2.6. Experiment 4: Mean percentages of hits and false alarms, and mean d' and c scores for peripheral target detection as a function of perceptual load at fixation and of peripheral target timing (numbers in parentheses represent 1 standard error of the mean)

Perceptual load	Peripheral target timing	Hit rate (%)	FA rate (%)	d'	c
Low	Simultaneous	80 (3.1)	4.8 (2.9)	2.92 (0.27)	0.56 (0.08)
Low	Non-simultaneous	78.2 (2.7)	5.2 (2.8)	2.82 (0.28)	0.59 (0.09)
High	Simultaneous	77 (3.2)	4.8 (2.8)	2.76 (0.27)	0.61 (0.07)
High	Non-simultaneous	74.3 (3.4)	6.1 (3.7)	2.61 (0.3)	0.62 (0.07)

FA = false alarm

indicating reduced sensitivity under high perceptual load (**Table 2.6**). There was no main effect of timing ($F_{(1,10)} = 1.322$, MSE = 0.131, *ns*), and no interaction between load and timing ($F_{(1,10)} < 1$, *ns*). For hit rates, there was a main effect of load ($F_{(1,10)} = 6.083$, MSE = $2.18*10^{-3}$, p = 0.033), indicating lower hit rates under high load. There was no main effect of peripheral target timing ($F_{(1,10)} = 1.763$, MSE = $3.19*10^{-3}$, *ns*) and no interaction ($F_{(1,10)} < 1$, *ns*). For false alarms there were no significant effects (load: $F_{(1,10)} < 1$, *ns*; timing: $F_{(1,10)} = 2.347$, MSE = $3.74*10^{-4}$, *ns*; interaction: $F_{(1,10)} < 1$, *ns*). There were also no significant effects for the criterion measure c ($F < 1$ for load, timing and their interaction).

These results clearly show that while attentional resources were being consumed by high central perceptual load, visual sensitivity in the periphery decreased. Importantly, this effect occurred independently of the simultaneous physical presence of a central stimulus. This demonstrates that the effect of perceptual load at fixation on visual sensitivity in the periphery was the result of lower levels of attention being continuously deployed to the periphery under high

load, rather than just during competition from simultaneously-presented central stimuli.

2.6 Experiment 5

2.6.1 Introduction

The results of Experiment 4 showed that the depletion of attentional resources under high perceptual load at fixation – rather than the mere presence of a competing stimulus – leads to a reduction in peripheral visual sensitivity. It should be noted that under high perceptual load, peripheral target presentation in the non-simultaneous condition occurred within the period in which the central stimulus was being processed. This can be inferred from the fact that the mean RT to central targets under high load (nearly 600 ms) was longer than the difference between the onsets of peripheral targets and the central stimuli preceding them (500 ms). The recruitment of attentional resources by central stimuli may therefore occur within a limited temporal window following each central stimulus. Hence, even in the context of continuous high-load central target detection, sensitivity to peripheral stimuli presented outside this window may improve compared to presentations within the window. Alternatively, it is possible that the effects of load observed in Experiments 1 to 4 simply reflect strategic effects due to attentional set (e.g., Theeuwes, Kramer & Belopolsky, 2004), with central stimuli being prioritized over peripheral ones to a greater extent under high perceptual load. If this is the case, the temporal asynchrony

between central stimulus and peripheral target onset should not matter.

Therefore, in this experiment the inter-stimulus-interval of the central stimuli was lengthened to 750 ms (compared with 500 ms in the previous experiments), to allow for the inclusion of a period of time after the processing of the central stimulus has ended (~600 ms under high load) where attentional resources should be free for deployment to the periphery. Peripheral stimuli were presented at two possible points within the inter-stimulus-interval: Either 500 ms after central-stimulus onset (near condition, similar to the non-simultaneous condition of Experiment 4, and within the processing window of the central stimuli under high load), or 750 ms after central-stimulus onset (far condition). If the engagement of attentional resources in central-stimulus processing is indeed the cause of the perceptual load effect, then this effect should be replicated for the near, but not the far condition, leading to an interaction between load and peripheral target timing.

2.6.2 Method

Participants: Twelve new volunteers took part in the experiment. One participant was excluded from the analysis due to poor central target detection (<70% under high load) and one for slow RTs to central targets (mean under high load: 790 ms), which meant his responses were given within the timeframe of the far condition, which was designed to occur after processing of the central stimulus was over. The remaining ten participants had a mean age of 25.8 (range

21-34). Five were female and nine were right handed. All had normal or corrected-to-normal vision.

Stimuli, design and procedure: These were identical to those of Experiment 4, except for the following differences. The inter-stimulus interval for central stimuli was 750 ms (an SOA of 1000 ms), as opposed to 500 ms (or a 750 ms SOA) in the previous experiments. Additionally, peripheral targets were never presented simultaneously with central stimuli. They were presented either 500 ms after central-stimulus onset (near condition, similar to the non-simultaneous condition of Experiment 4), or 750 ms after central stimulus onset (far condition; see **Figure 2.5**). The experiment therefore had a 2 (load: low, high) by 2 (peripheral target timing: near, far) factorial design.

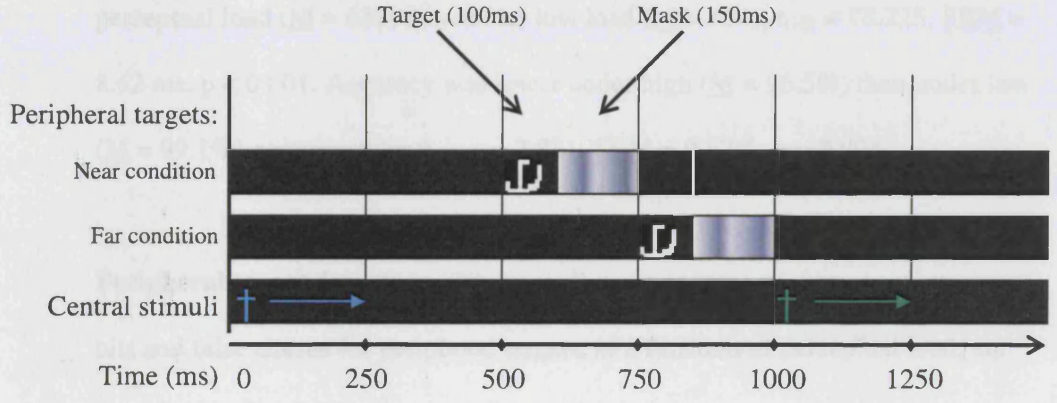

Figure 2.5. Experiment 5: Schematic timeline of the central and peripheral stimulus presentations. The SOA of the central stimuli in this experiment was 1000 ms (as opposed to 750 ms in the previous experiments). The near condition was similar to the non-simultaneous condition of Experiment 4, with peripheral target onset 500 ms after the onset of a central stimulus. In the far condition peripheral target onset was 750 ms after central stimulus onset. In the actual experiment only a single peripheral target could appear in the interval between two central stimuli.

As in the previous experiments, half of the peripheral stimuli were masks not preceded by a peripheral target. Timing of masks was the same (600 and 850 ms after central-stimulus onset for the near and far conditions, respectively) regardless of whether they were preceded by a peripheral target or not. The longer SOA between central stimuli meant each trial was longer than in the previous experiments (64 versus 48 s). Therefore, the experiment comprised only six (rather than eight) blocks of trials. The total number of peripheral targets was roughly the same as in the previous experiments, though, as peripheral targets were presented with the same frequency as in Experiments 3 and 4 (i.e. a 5 s minimum between peripheral target presentations in the same location).

2.6.3 Results and discussion

Central target detection: Mean RTs were again longer under high perceptual load ($\underline{M}$ = 622) than under low load ($\underline{M}$ = 464), $t_{(10)} = 18.225$, $\underline{SEM}$ = 8.62 ms, $p < 0.001$. Accuracy was lower under high ($\underline{M}$ = 96.5%) than under low ($\underline{M}$ = 99.1%) perceptual load, $t_{(10)} = 3.881$, $\underline{SEM}$ = 0.67%, $p = 0.004$.

Peripheral target detection: The mean d' and c scores and mean percentages of hits and false alarms for peripheral targets, as a function of perceptual load, are presented in **Table 2.7**. d' scores, hit and false alarm rates and c scores were entered into 2 (perceptual load: low, high) by 2 (peripheral target timing: near, far) repeated-measures ANOVAs. Critically, for d' scores there were no main effects (load: $F_{(1,9)} < 1$, *ns*; timing: $F_{(1,9)} = 1.17$, $\underline{MSE}$ = 0.121, *ns*), but there was a significant interaction ($F_{(1,9)} = 12.018$, $\underline{MSE} = 2.55*10^{-2}$, $p = 0.007$). Paired

Table 2.7. Experiment 5: Mean percentage hits and false alarms and mean d' and c scores for peripheral target detection as a function of perceptual load at fixation and of peripheral target timing (numbers in parentheses represent 1 standard error of the mean)

Perceptual load	Peripheral target timing	Hit rate (%)	FA rate (%)	d'	c
Low	near	75.1 (3.6)	1 (0.6)	3.06 (0.21)	0.80 (0.07)
Low	far	76.2 (3.3)	1.1 (0.3)	3.01 (0.14)	0.78 (0.06)
High	near	67.8 (3.9)	1.3 (1.1)	2.83 (0.19)	0.93 (0.08)
High	far	76.5 (3.6)	1 (0.7)	3.13 (0.19)	0.79 (0.06)

FA = false alarm

sample t-tests revealed that the interaction was driven by a strong effect of load in the near condition ($t_{(9)} = 2.451$, SEM = 0.095, $p = 0.037$), indicating a reduction in sensitivity under high load, coupled with the absence of an effect in the far condition ($t_{(9)} < -.96$, *ns*). For hit rates there was no main effect of timing ($F_{(1,9)} = 1.845$, MSE = $1.3*10^{-2}$, *ns*), but there was a main effect of load ($F_{(1,9)} = 5.803$, MSE = $2.11*10^{-3}$, $p = 0.039$), and importantly, there was a significant interaction between load and timing ($F_{(1,9)} = 15.271$, MSE = $9.46*10^{-4}$, $p = 0.004$). Paired-sample t-tests revealed that whereas in the near condition there was a strong effect of load ($t_{(9)} = 4.168$, SEM = 0.017, $p = 0.002$), this effect was completely absent in the far condition ($t_{(9)} < -.172$, *ns*). There were no significant effects for either false alarms, (load: $F_{(1,9)} < 1$, *ns*; timing: $F_{(1,9)} < 1$, *ns*; interaction: $F_{(1,9)} = 2.25$, MSE = $1.78*10^{-5}$, *ns*) or the criterion measure c (load: $F_{(1,9)} = 3.962$, MSE = $1.34*10^{-2}$, *ns*; timing: $F_{(1,9)} = 1.34$, MSE = $4.88*10^{-2}$, *ns*; interaction: $F_{(1,9)} = 4.817$, MSE = $8.24*10^{-3}$, *ns*).

As predicted, the results of the present experiment replicate the effect of perceptual load at fixation on visual sensitivity in the periphery for the near, but not the far condition. This confirms that the effect of load indeed reflects the depletion of attentional resources during processing of the central stimulus. When this processing is finished, attention levels – and therefore sensitivity – are no longer reduced in the periphery. These results rule out the possibility that strategy, or attentional set (Theeuwes et al, 2004) determine performance in the different perceptual load conditions.

2.7 Chapter Discussion

The results of the present study demonstrate a clear relationship between attention and perceptual awareness, thus addressing the question posed at the beginning of this chapter regarding the extent to which conscious perception depends on attention. Furthermore, they establish that the predictions of load theory (Lavie 1995, 2005) hold not only for perceptual processing (which may or may not be conscious) but for visual awareness as well. Manipulating perceptual load at fixation modulated conscious awareness of concurrently-presented peripheral stimuli: Experiments 1 and 2 established that under high (compared to low) central perceptual load, visual sensitivity in the periphery is reduced. Experiment 3 showed that this effect is indeed due to a reduction in attentional capacity, rather than the need to coordinate attention and inhibition in different locations. Experiment 4 confirmed that the effect of load is independent of the physical presence of a competing central stimulus, by replicating the effect for

peripheral targets presented in the absence of any other stimuli. Finally, Experiment 5 showed that the effect of load indeed reflects the depletion of attentional resources during processing of the central stimulus, rather than an effect of strategy. Taken together, these results support a view of visual awareness as a function of available processing resources. As proposed by load theory, the level of available perceptual capacity influences whether or not a visual stimulus will reach awareness.

The effects of perceptual load on indirect measures of stimulus detection, such as RTs and stimulus-evoked neural activity, have been demonstrated before (Beck & Lavie, 2005; Lavie, 1995; Lavie & Cox, 1997; Lavie & Fox, 2000; Pessoa et al, 2002; Pinsk et al, 2003; Rees et al, 1997; Schwartz et al, 2005; Yi et al, 2004). However, a direct effect of load on visual awareness has previously been demonstrated only by showing a load effect on inattentional blindness (Cartwright-Finch & Lavie, 2006). While those results were suggestive of the role of attention in visual awareness, the present study overcomes various problems associated with the inattentional blindness paradigm. The possibility that inattentional blindness reflects rapid forgetting of an unexpected stimulus (Barber & Folkard, 1972; Bashinski & Bacharach, 1980; Davies et al, 1983; Teichner & Krebs, 1974 ; Wolfe, 1999) was avoided by using stimuli that were fully expected, and by being able to collect responses to these stimuli immediately (and not following another response, as in inattentional blindness) due to using a continuous monitoring paradigm where the two types of target were never presented simultaneously.

Previous research has suggested that divided attention only leads to reduced performance when targets appear in a display simultaneously and require

independent identification and a separate response (Duncan, 1980). The non-simultaneity of the two types of target in all five experiments of this chapter (and of central and peripheral stimuli in Experiments 4 and 5) rules out any explanation of the results in terms of such a two-target cost.

The results can also not reflect a de-prioritization of responding to peripheral targets under high load (goal neglect), as this would have led to fewer false alarms in addition to the decline in hit rates, leading to an effect of load on the criterion measure c – but in fact the trend was for more false alarms under high load, and load had no effect on criterion in all five experiments.

Finally, the present paradigm also made it possible to individually assess hit and false alarms rates. This made it possible to calculate an objective, unbiased measure of visual sensitivity for each participant under both low and high perceptual load (rather than simply collecting a single data point indicating a hit or a miss, as in inattentional blindness).

Though the present results are predicted by load theory, they seem to contradict previous evidence supporting the claim that though visual discrimination requires attentional capacity, detection occurs in a capacity free, automatic manner: When two visual discrimination tasks are performed concurrently, performance on one task comes at the expense of performance on the other – but when one of the tasks involves simple detection, there is no such decline in performance (Braun, Koch, Lee, & Itti, 2001). Similarly, detection of luminance increments seems to be capacity free, whereas discriminating luminance increments from decrements depends on the allocation of attention (Bonnel, Stein, & Bertucci, 1992). However, in neither of the above cases was perceptual load manipulated directly. This precludes conclusions regarding the

role of load in perception. Furthermore, the stimuli used in these studies were highly salient and unlikely to test the limitations of the visual system.

More relevant, perhaps, are the results of experiments that also used salient stimuli but compared single with dual-task performance: Braun & Sagi (1990; 1991) showed that the detection of a differently-oriented line that pops out of a uniformly oriented texture does not seem to decline with the addition of a concurrent discrimination task, whereas the discrimination of different orientations does (see also Sagi & Julesz, 1985a; 1985b). However, a later study (Joseph, Chun & Nakayama, 1997) showed that while oriented-line detection is indeed unimpaired under dual-task compared to single-task conditions when the other task involves orientation discrimination, a dual-task cost does arise when the other task is a demanding RSVP letter task. This implies that a sufficient level of demands on attention can indeed reduce detection performance for other, concurrent stimuli. With regard to the findings presented here, it is also important to remember that a single versus dual-task manipulation does not parallel perceptual load manipulations. The addition of a task affects not only the load on attention, but also adds demands on response production and memory, which may cause effects accounted for in terms of goal neglect, reprioritization of tasks and postponement of responses to secondary task stimuli which could lead to a higher probability of memory decay. The results presented in this chapter, on the other hand, demonstrate an effect of perceptual load on visual sensitivity which cannot be explained by any of these alternative accounts. These results, therefore, provide direct evidence that conscious perception depends on the allocation of limited-capacity attention, and that depleting attentional resources by imposing high perceptual load on one stimulus can reduce awareness of another.

Chapter 3:

The effect of perceptual load on the temporal resolution of visual awareness

3.1 Chapter Introduction

In the previous chapter, I employed a perceptual load manipulation (Lavie 1995, 2005) to establish that the availability of processing resources influences visual awareness. In the series of experiments described in that chapter, detection of particular shapes in specific spatial locations was required. But subjective experience of the physical world depends not only on the spatial arrangement of the environment. It also depends on the temporal pattern of stimulation. For example, flickering and steady light can be presented in the same location yet evoke a very different conscious experience due to their different temporal patterns. Does attention play a role in temporal aspects of visual awareness? In this chapter I use perceptual load to investigate whether the availability of processing resources affects the temporal resolution of visual awareness – the ability to distinguish rapid changes in light intensity, thus detecting temporal patterns embedded in visual stimuli (Levine, 2000; Yeshurun & Levy, 2003; Yeshurun, 2004).

Although the temporal pattern of visual stimulation clearly has a great influence on our subjective experience of the world, surprisingly little research (compared to the amount of research on attention to spatial patterns) has attempted to directly investigate the effects of attention in this domain. This could be due to our subjective experience of time as a continuous, seamless perceptual dimension. But does this intuition reflect the way the visual system works? It is indeed conceivable that the temporal aspects of visual perception are continuous and capacity-free – that is, limited only by the firing-rate ceiling of

visual neurons. If this is the case, attentional manipulations should not affect the visual system's ability to perceive temporal patterns.

On the other hand, it has been suggested that rather than being continuous, visual awareness relies on discrete processing epochs, or 'snapshots' (Crick & Koch, 2003; VanRullen & Koch, 2003). Research supporting this proposition includes the finding that the 'wagon-wheel illusion' – in which wheels in movies or under stroboscopic lighting conditions may appear to rotate backwards – can also occur in real life under natural lighting (Purves, Paydarfar, & Andrews, 1996). This has been interpreted as indicating that normal motion perception consists of processing a series of separate snapshots (Crick & Koch, 2003). Recently, this illusion has been shown to be modulated by attention, almost disappearing in the absence of focused attention (VanRullen, Reddy & Koch, 2005). But though this finding demonstrates that attention can modulate the way temporal information is integrated within a spatial pattern, it does not shed light on the extent to which attention is necessary in the actual detection of temporal patterns.

In a different study, an attentional blink paradigm was used to observe the effects of limited attentional capacity on temporal integration (the ability to combine different stimuli separated by a temporal gap into a single unified percept; Visser & Enns, 2001). In the attentional blink two targets are presented, separated by a brief temporal interval, and participants are required to identify both. Identification of the second target is severely impaired if it is displayed a short time (usually less than 500 ms) after the first target (Shapiro et al, 1998). Detection of the second target is worse the shorter the lag between the first and second target, a finding that has been attributed to attentional resources being

consumed by the first target, rendering them temporarily unavailable to process the second target (Chun & Potter, 1995; Shapiro et al, 1998). Visser and Enns (2001) used this phenomenon to demonstrate that when task performance for the second target depended on temporally integrating two images (temporally-separate dot-matrices which together formed the second target – a square with one missing dot that had to be spatially localized), a typical attentional blink pattern was found, with performance improving as the lag from the first target increased. The greater attentional availability increased both accuracy and the duration over which successive stimuli could be integrated. Attentional resources, therefore, play a role in temporal integration. But temporal integration of spatial patterns (perceptually unifying temporally distinct events) is not the same as temporal resolution (being able to tell such events apart).

Another recent study (Carrasco & McElree, 2001) showed that transient attention, induced for a brief duration by a spatial cue, accelerates the rate of information processing for stimuli appearing at the cued location. Carrasco & McElree (2001) asked participants to report a stimulus attribute (e.g., grating orientation). Rather than collecting RTs, they had participants respond after one of several latencies from stimulus presentation, and found that accuracy at short latencies was better for cued stimuli. However, the increase in processing speed observed by Carrasco & McElree (2001) was obtained for attended stimuli (gratings), which were again not temporal patterns themselves. These findings may therefore reflect faster processing of attended static patterns, which does not necessarily mean that attention alters the rate at which visual information is perceived (i.e., the speed at which separate events can be distinguished – the temporal resolution of the visual system).

Perhaps most pertinent to the current chapter is a recent set of studies which demonstrated that spatial attention can actually impair the temporal resolution of vision (Yeshurun & Levy, 2003; Yeshurun, 2004). These studies investigated the effect of transient attention on observers' ability to detect a temporal gap (rapid disappearance and reappearance) in a stimulus. Interestingly, and in contrast to the findings of Carrasco & McElree (2001), these studies found that the ability to detect such temporal events at cued locations was impaired compared to performance at uncued locations. The authors' proposed explanation for this effect was that spatial cuing facilitates the activity of parvocellular neurons in retinotopic regions corresponding to the attended location, which in turn leads to inhibition of magnocellular neurons at the same location. Parvocellular neurons have smaller receptive fields than magnocellular neurons, allowing attended locations to enjoy improved spatial resolution; but they also have longer response durations than magnocellular neurons (Merigan & Maunsell, 1993; Schiller & Logothetis, 1990), leading to lower temporal resolution. This account offers a plausible mechanism by which spatial cuing evokes transient attention. Importantly, however, transient attention is reflexively drawn to the cue in a bottom-up manner for a limited duration (less than 250 ms; Carrasco & McElree, 2001). Whether or not similar mechanisms mediate the effects of top-down, goal-driven resource-dependent attention remains unclear. Furthermore, transient attention is evoked by a cue toward a specific spatial location, confounding attention to a spatial location with attention to temporal patterns.

The finding that transient attention impairs temporal resolution leads to the prediction that when attentional resources are reduced, the ability to detect temporally-distinct events should improve (as there would be less parvocellular

activity at attended locations, and therefore less inhibition of magnocellular activity). This is at odds with load theory (Lavie, 1995; 2005), which does not distinguish between spatial and temporal patterns, and predicts that exhausting attentional resources should impair perception in both the spatial and temporal domains.

The purpose of the present series of experiments was therefore to investigate this issue by manipulating perceptual load for shapes, and examining the effect this had on conscious awareness of flicker presented at fixation. Flicker is a rapid train of discrete luminance changes, and thus makes a good tool for studying temporal aspects of vision (Wells, Bernstein, Scott, Bennett, & Mendelson, 2001). When sufficiently fast, the luminance changes of flicker are no longer perceived as flickering but as steady, or fused, illumination (Curran & Wattis, 1998; Kristofferson, 1967). At the Critical Flicker Fusion (CFF) threshold (~25-50Hz, depending on specific conditions; Andrews, White, Binder, & Purves, 1996; Curran & Wattis, 1998; Kristofferson, 1967), a flickering light has an equal probability of being perceived as flickering or fused. The same physical stimulus – flicker at the CFF threshold – can therefore give rise to two different percepts. This is an example in the temporal domain of a dissociation between physical stimulation and perceptual outcome – the hallmark of phenomena considered particularly useful in the study of perceptual awareness (like binocular rivalry or change blindness in the spatial domain; Blake & Logothetis, 2002; Frith, Perry & Lumer, 1999; Rees et al, 2002). Furthermore, the involvement of spatial patterns in the processing of flicker can be minimized with the use of a small, fixated point-source of light, where only the temporal pattern will determine the qualitative nature (flicker or fused) of the percept.

Like conscious awareness of shapes (Chapter 2), awareness of flicker may depend on attentional resources. However, it is possible that awareness of flicker may actually be improved by the depletion of such resources (Yeshurun & Levy, 2003; Yeshurun, 2004). It is also possible that the rapid serial onsets of flicker attract attention in a bottom-up fashion, rendering directed attention unnecessary for flicker awareness. Moreover, it has been suggested that the spatial and temporal dimensions of visual stimuli are processed independently (Lehky, 1985; Wilson, 1980), which would mean that a manipulation of perceptual load using shapes in particular locations, as in Chapter 2, would not affect temporal awareness.

To investigate whether visual awareness of temporal patterns requires processing resources (or, conversely, is impaired by their availability, as suggested by Yeshurun & Levy, 2003), in the present series of experiments participants were asked to detect flicker in a fixated light-emitting diode (LED) which flickered at or around the individually-adjusted CFF threshold, while searching for a target letter presented either on its own (low load) or among other letters (high load) in the periphery. Previous research (Lavie & Cox, 1997; Lavie & Fox, 2000) has established the effectiveness of this manipulation of perceptual load, demonstrating that it modulates the processing of distractors. If processing resources are required for conscious awareness of flicker, then reducing the availability of such resources by increasing perceptual load should impair perception of threshold-level flicker.

3.2. Experiment 6

3.2.1. Introduction

Participants fixated a red LED mounted on the centre of a computer screen. On each trial, participants were briefly presented with a target letter in the periphery and asked to report whether this letter was an X or an N. The target letter could appear in one of six locations, arranged in a hexagon around fixation. Under low perceptual load the other five locations were occupied by small circles; under high load, they were occupied by non-target letters. The fixated LED flickered simultaneously with the peripheral letter presentation, at or around participants' individually-assessed CFF threshold (see Method below). After reporting the identity of the target letter, participants reported whether or not they had perceived the LED to be flickering. If perceptual load in a spatial search affects flicker perception at fixation, then for the same frequencies participants should report flicker percepts on fewer trials under high than under low perceptual load.

3.2.2. Method

Participants: Six volunteers participated in the experiment. Their mean age was 30.3 (range 22-44), three were female and five were right-handed. All had normal or corrected-to-normal vision.

Stimuli and apparatus: Participants sat in a room with ambient lighting, viewing a 14'' screen (Dell D825TM, resolution 640*480, 60 Hz refresh rate) from a distance of 57 cm. Head position was stabilized by a chin rest. Stimuli were created and presented using Matlab on a Dell Inspiron 4000 computer.

During the experiment, the stimulation on each trial consisted of flicker events at fixation and letter presentations in the periphery. Flicker and letter presentations were simultaneous. Participants fixated a single red LED (CIE chromaticity coordinates x=0.655, y=0.344) which was mounted at the centre of the screen and subtended 0.5° visual angle. On each trial the LED would flicker (square-wave flicker, 1:1 duty cycle; luminance 29 cd/m^2 at 30 Hz).

Letter stimuli consisted of a target letter (an uppercase X or N), which could appear in any one of six locations (the vertices of a perfect hexagon, each 2.9° from fixation). Under low perceptual load, small place-holder circles (diameter 0.2°) appeared in the other five locations. Under high perceptual load, the other five locations were occupied by non-target uppercase letters (always the letters U, F, S, P & J, placed randomly; see **Figure 3.1**). Letter dimensions were 0.7° vertically by 0.5° horizontally. Letters and place holders were presented in white on a black background.

Critical flicker fusion threshold measurement: The CFF threshold (the frequency at which a flickering light has an equal probability of being perceived as flickering or fused) was measured for each participant individually at the beginning of the experimental session, using the method of constant stimuli. This assessment consisted of 120 trials in which flicker events were presented on their own (without concurrent letter presentations as in the experiment). Flicker events

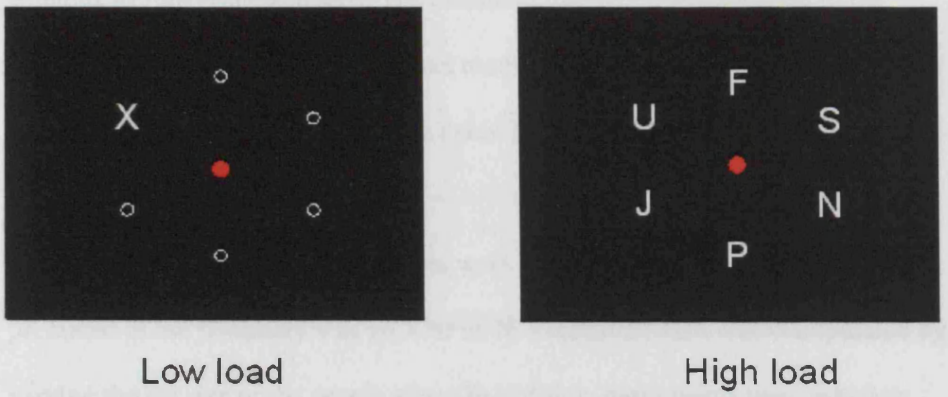

Figure 3.1. Experiment 6: Schematic illustrations of the visual stimuli. On each trial, a flicker event in the centrally-fixated red LED (represented here by a red circle) was presented simultaneously with peripheral letters. Under low perceptual load (left), a single target letter (in this case X) was presented at one of six locations. Small circular place-holders were presented at the other five locations. Under high load (right), the target (in this case N) was accompanied by five other letters at the other five locations. Figure not to scale.

at 6 different frequencies were presented in random order (26 to 36 Hz, in steps of 2 Hz; 20 trials for each frequency). The duration of each flicker event was 200 ms, and participants were given 2500 ms from stimulus onset to report whether they perceived the light to be flickering or fused (by pressing the left arrow key for 'flicker' and the down arrow for 'fused') before the next stimulus was presented. Participants were informed that the LED would illuminate briefly on each trial, and would sometimes flicker; they were not told that the stimulus would always, in fact, be flickering, or that the same frequency may lead to different percepts. This part of the experimental session was described to participants as practice in distinguishing flicker and fused illumination. The data obtained were used to estimate the participant's threshold frequency (the frequency at which the participant would be equally likely to categorize the

stimulus as flickering or fused). The threshold frequency was rounded to the nearest whole number, which was then used to determine the frequencies displayed during the experiment (see below).

Design: On each trial, participants were asked whether a target letter presented in the periphery was an X or an N. Perceptual load was manipulated by varying the set size of the search array. In addition, participants were asked to report whether they had perceived the illumination of the fixated LED, which occurred simultaneously with the letter presentation, as flickering or fused. Pilot tests revealed that when combined with letter detection, the CFF threshold was lower compared to the threshold assessment. To accommodate this, the threshold frequency in the experiment was therefore set to 3 Hz lower than that found in the threshold measurement procedure. Three frequencies were used in the experimental conditions to prevent a constant response[1]: The adjusted threshold, and frequencies 1 Hz lower and 1 Hz higher.

Two factors were therefore manipulated independently in a factorial design: Perceptual load (two levels: low or high), and flicker frequency (three levels: threshold, and frequencies 1 Hz below and above threshold). The main dependent variable was the percent of trials in which the flicker event was categorized as 'flicker'.

[1] A preliminary study revealed that even when shown the pre-assessed threshold frequency, participants tended to adopt a constant response if only a single frequency were used in all trials.

Procedure: The experiment was conducted in a single session lasting about 1.5 hours. Before the experiment itself, participants underwent the CFF threshold measurement, followed by a short practice.

In each trial of the experiment, the letter and flicker stimuli were presented simultaneously for 200 ms. The brief presentation was intended to prevent eye movements to the letter target, and the foveal presentation and brief duration of the flicker minimized temporal adaptation effects (Curran & Wattis, 1998). At the end of the presentation the screen went black. A response window of 1500 ms from stimulus onset was given to report the letter. Participants pressed the left arrow to report an 'X' and the down arrow for an 'N'. At the end of the response window (regardless of whether a response had been made), the question 'Flicker or fused?' appeared on the screen above the LED and remained until a response was given. Participants responded by pressing the same keys, but this time the left arrow was used to report flicker and the down arrow was used to report a fused percept. An inter-trial interval of 500 ms followed response to the flicker (see **Figure 3.2**).

Perceptual load conditions were blocked. Participants performed two practice blocks (one under each load condition), followed by eight experimental blocks. Blocks were arranged in an ABBABAAB order (with A representing low and B high perceptual load, or vice versa). The load of the first block was counterbalanced across participants. Each block comprised 96 trials, containing two repetitions of the 36 possible combinations of letter identity (X or N), letter location (6 possible locations) and three flicker frequencies. In addition, there were 24 catch trials. On half of these the flicker frequency was 12 Hz below the threshold and on half it was 12 Hz above threshold. These were used to control

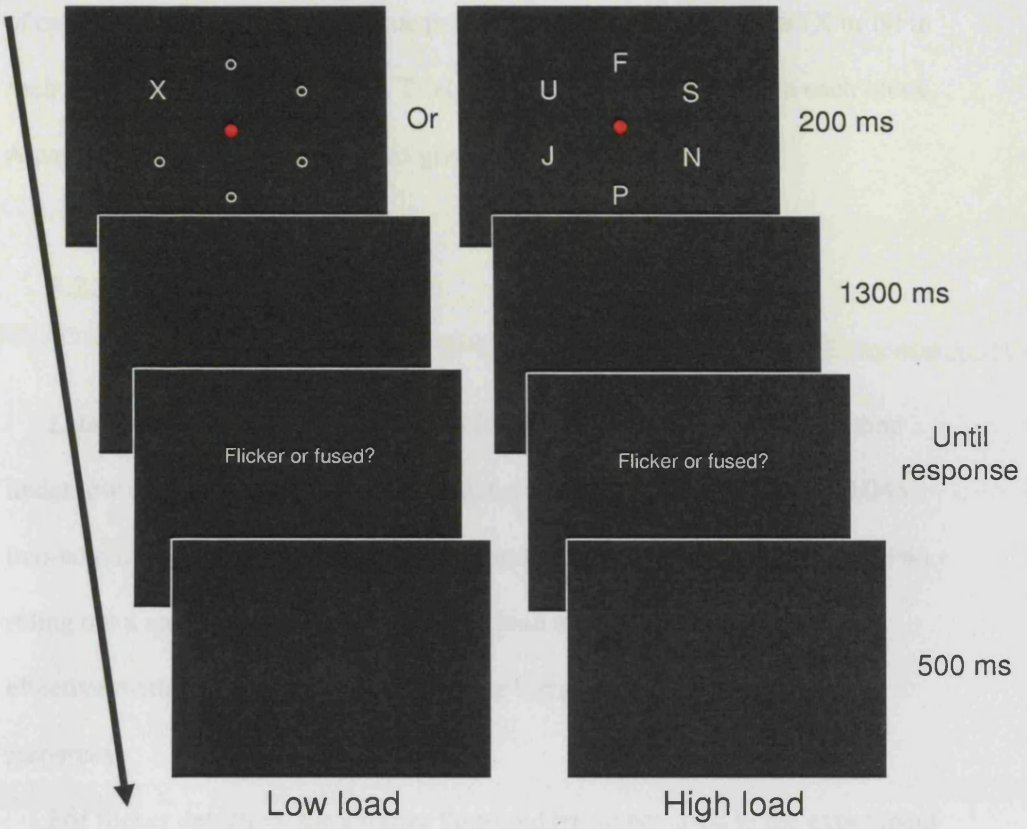

Figure 3.2. Experiment 6: Trial sequence. Each trial began with the simultaneous presentation of letter stimuli in the periphery and LED flicker at fixation for 200 ms. A response window of 1500 ms from stimulus onset (during the last 1300 ms of which the screen was black) was given for the letter search. This was followed by a prompt for response to the flicker, which remained on the screen until a response was given. The trial ended with a 500 ms inter-trial interval. Figure not to scale.

for possible response biases and to make sure participants were attending to the task. For both load conditions, these frequencies were expected to be far enough from threshold to ensure that if participants were indeed attending to the flicker, they would almost never report flicker for the threshold plus 12 Hz frequency, and nearly always do so for the threshold minus 12 Hz frequency. For each kind

of catch trial, the trials included one presentation of each target letter (X or N) in each of the six possible locations. Trial order was randomized within each block. A participant-terminated break was given at the end of each block.

3.2.3. Results and discussion

Letter search RTs were significantly longer under high (M = 866 ms) than under low (M = 807 ms) perceptual load; $t_{(5)} = 2.699$, SEM = 21.83; $p = 0.043$, two-tailed. Accuracy rates were identical under both load conditions (M = 94%), ruling out a speed/accuracy trade-off. The load manipulation was therefore effective, with high perceptual load placing higher demands on perceptual resources.

For flicker detection, the average threshold frequency used in the experiment was 27 Hz (range 25-28 Hz). Only trials in which a correct response in the letter search was made were used in the analysis of flicker detection in all the experiments reported in this chapter. The percentages of flicker responses were entered into a 2 (Perceptual load: low or high) by 3 (Flicker frequency: threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated-measures ANOVA. There was a significant main effect of perceptual load ($F_{(1,5)} = 15.918$, MSE = $7.62*10^{-3}$, $p = 0.01$), indicating a reduction in flicker perception under high, compared to low load (M = 35% versus 47% under high and low load, respectively, when collapsed across all three frequencies; see also **Figure 3.3**). There was also a significant main effect of frequency ($F_{(2,10)} = 20.317$, MSE = $1.78*10^{-2}$, $p < 0.001$), demonstrating an increase in flicker responses as

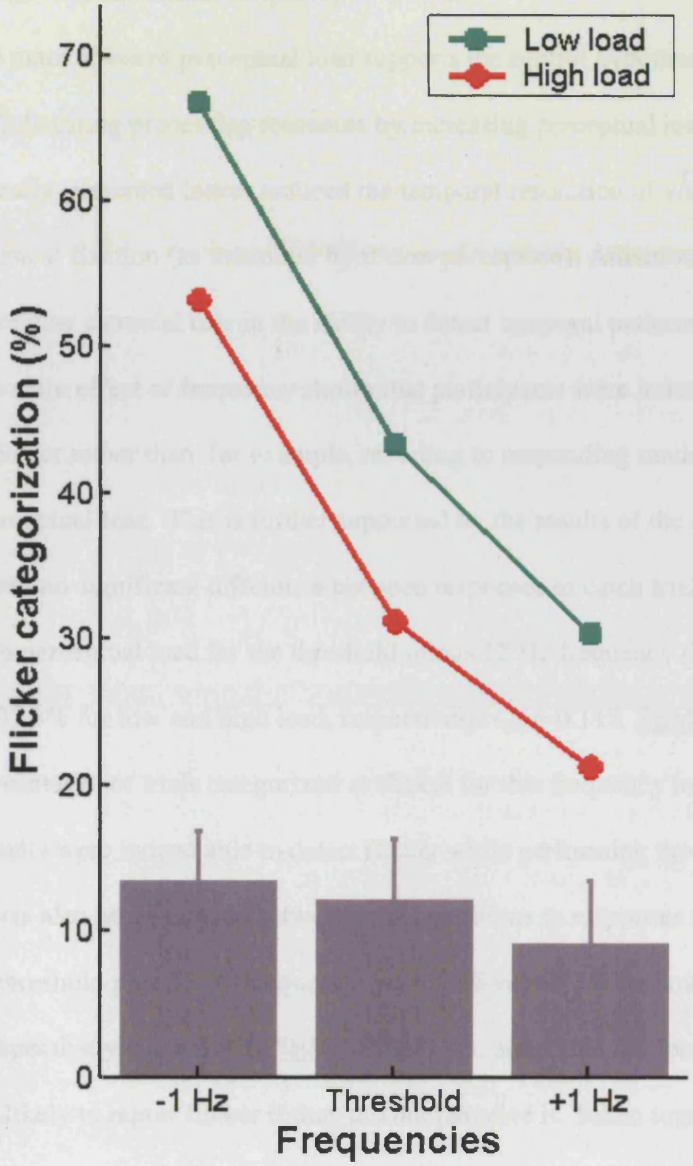

Figure 3.3. Experiment 6: Flicker detection results. Mean flicker categorization rates were lower under high (red circles) than under low (green squares) perceptual load. Flicker detection also decreased as frequency increased. The grey bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

frequency was reduced (**Figure 3.3**). There was no interaction between perceptual load and flicker frequency ($F < 1$, *ns*).

The main effect of perceptual load supports the central hypothesis of this study. Exhausting processing resources by increasing perceptual load for the peripherally-presented letters reduced the temporal resolution of visual awareness at fixation (as measured by flicker perception). Attention may therefore play a crucial role in the ability to detect temporal patterns in vision.

The main effect of frequency shows that participants were indeed attending to the flicker rather than, for example, reverting to responding randomly under high perceptual load. This is further supported by the results of the catch trials: There was no significant difference between responses to catch trials under low and high perceptual load for the threshold minus 12 Hz frequency ($\underline{M}$ = 97.1% versus 97.3% for low and high load, respectively; $t_{(5)} = 0.115$, $\underline{SEM} = 0.014$, *ns*). The percentages of trials categorized as flicker for this frequency indicate that participants were indeed able to detect flicker while performing the letter search. There was also no difference between load conditions in responses to catch trials for the threshold plus 12 Hz frequency ($\underline{M}$ = 10% versus 7% for low and high load, respectively; $t_{(5)} = 0.656$, $\underline{SEM} = 0.048$, *ns*), indicating that participants were unlikely to report flicker if they did not perceive it. Taken together, the present results clearly demonstrate that increasing perceptual load in the peripheral letter search decreased flicker perception at fixation.

However, although the catch trial performance rules out a gross response bias, it remains possible that more subtle biases were induced by perceptual load at the threshold frequencies. This issue was addressed in Experiment 7.

3.3. Experiment 7

3.3.1. Introduction

In Experiment 6, the perception of flicker at fixation was impaired under high perceptual load. Participants in that experiment made the letter search response before the flicker detection response. This was necessary in order to establish that the perceptual load manipulation was indeed effective, leading to longer RTs under high (compared to low) load. However, it is possible that the effect of perceptual load on flicker perception was due to the delayed response to flicker. For example, the longer time it took participants to report the target letter under high load may have led to a weaker memory trace for the intended flicker report. In addition, high perceptual load may have led to reduced prioritisation (goal neglect) of the second response on each trial. In either of these cases, if participants were biased toward reporting a fused percept when they were uncertain, this could account for the observed results.

Another alternative account for the results of Experiment 6 is that because small circular place-holder stimuli (rather than full-size letters) were used in the low load condition, the total luminance of the letter stimuli was lower under low than under high perceptual load. It is therefore possible that the effect of load found in Experiment 6 is in fact due to this low-level difference between load conditions, as flicker may be harder to detect under conditions of greater illumination.

These possibilities were addressed in Experiment 7 by switching the order in which the letter search and flicker detection responses were given, and replacing

the small place-holders in the low load condition with the letter 'O'. In all other respects, this experiment was identical to Experiment 6. If the results of Experiment 6 were indeed due to the effect of perceptual load (rather than being a memory-related artefact or the by-product of luminance differences between conditions), they should be replicated here.

3.3.2. Method

Participants: Six new volunteers took part in the experiment. Their average age was 23.7 (range 19-28). Five were female, and all were right-handed and had normal or corrected-to-normal vision.

Stimuli, design and procedure: These were identical to those of Experiment 6 except for the following differences. First, the order of responses was switched. Participants responded to the flicker first, during the 1500 ms response window. Then the question 'X or N?' appeared on the screen and remained until a response to the letter search was given. Second, In the low perceptual load condition, the small, circular place-holders used in Experiment 6 were replaced by the letter 'O', so that the total size and luminance of visual features presented during each trial was similar under low and high load.

3.3.3. Results and discussion

Letter search RTs were not measured in this experiment, as on each trial responses to the flicker were made first. Accuracy rates, however, were

significantly better under low (M = 92.3%) than under high (M = 87.3%) perceptual load; $t_{(5)} = 2.459$, SEM = 0.02, $p = 0.028$.

For flicker, the average threshold frequency used in the experiment was 26 Hz (range 25-28 Hz). The percentages of trials in which the illumination of the LED was categorized as flicker were again entered into a 2 (Perceptual load: Low or high) by 3 (Flicker frequency: Threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated-measures ANOVA. There was a significant main effect of perceptual load ($F_{(1,5)} = 9.567$, MSE = $3.39*10^{-3}$, $p = 0.027$). This replicates the result of Experiment 6, showing that for the same frequencies, flicker was perceived less under high than under low perceptual load (M = 37.5% versus 31.8% under low and high load, respectively, when collapsed across all three frequencies; see also **Figure 3.4**). Though the magnitude of the effect of load was somewhat reduced compared to Experiment 6, these results conclusively rule out alternative explanations, accounting for the effect of load in terms of memory-related biases or deprioritization of the second response. The fact that letter stimuli in this experiment had similar luminance under both load conditions rules out the possibility that the results of Experiment 6 were due to low-level luminance differences.

As in Experiment 6, there was also a significant main effect of frequency ($F_{(2,10)} = 19.104$, MSE = $1.01*10^{-2}$, $p < 0.001$), indicating a decline in flicker perception rates as frequency increased (**Figure 3.4**). There was no interaction between perceptual load and flicker frequency ($F < 1$, *ns*).

Catch-trial results for the threshold minus 12 Hz frequency again showed that there was no significant difference in participants' ability to perceive and report flicker under both perceptual load conditions (95.2 and 92.7% for low and high

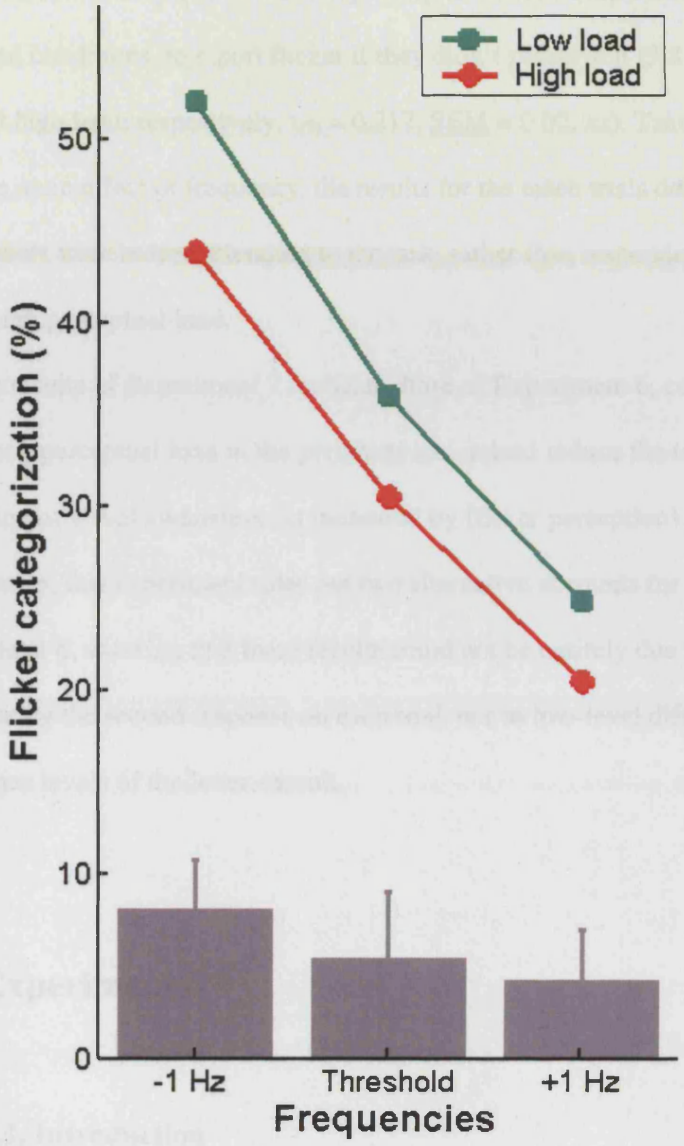

Figure 3.4. Experiment 7: Flicker detection results. As in Experiment 6, mean flicker categorization rates were lower under high (red circles) than under low (green squares) perceptual load. Flicker detection also decreased as frequency increased. The grey bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

load, respectively; $t_{(5)} = 1.185$, SEM = 0.02, *ns*). For the threshold plus 12 Hz catch trials, results again showed that participants were equally unlikely, under both load conditions, to report flicker if they didn't perceive it (3.8 and 3.3% for low and high load, respectively; $t_{(5)} = 0.217$, SEM = 0.02, *ns*). Taken together with the main effect of frequency, the results for the catch trials demonstrate that participants were indeed attending to the task, rather than responding randomly under high perceptual load.

The results of Experiment 7 replicate those of Experiment 6, confirming that increasing perceptual load in the periphery can indeed reduce the temporal resolution of visual awareness (as measured by flicker perception) at fixation. Importantly, this experiment rules out two alternative accounts for the results of Experiment 6, showing that these results could not be entirely due to the flicker report being the second response on each trial, nor to low-level differences in luminance levels of the letter stimuli.

3.4. Experiment 8

3.4.1. Introduction

Experiments 6 and 7 demonstrated that the temporal resolution of visual awareness is modulated by attention. When perceptual load in the periphery was increased, flicker detection rates at fixation decreased (for the same frequencies). However, it is still unclear which element of the process that gives rise to conscious awareness of flicker is affected by attentional manipulation. Like any

other sensory percept, flicker detection can be characterized in terms of signal detection theory (SDT). Under conditions of uncertainty (e.g., close to a sensory threshold) the conscious, reported percept is the result of both the visual system's sensitivity to the presence of a signal (in this case, whether there is a temporal pattern of onsets and offsets in the illumination) and the application of a criterion for classifying an event as either containing the signal (in this case, flicker) or not (fused; Macmillan & Creelman, 1991). In Experiments 6 and 7, the effect of perceptual load may have been the result of a reduction in the visual system's sensitivity to flicker under high load. Alternatively, the effect may have been due to a shift in the criterion for categorizing an event as flickering or fused, such that under high load participants were simply more reluctant than under low load to classify a near-threshold event as flicker.

In Experiment 8 I therefore used a 2-interval forced-choice (2IFC) paradigm to distinguish the effects of perceptual load on sensitivity from those on criterion. Rather than a single presentation containing flicker at fixation and a search-array in the periphery, each trial in Experiment 8 consisted of two consecutive presentations. Each of the displays contained a target letter, and the letter search now required participants to report whether the two displays contained the same target letter or a different one. Attention to the search array was thus required on both presentations. For the fixated LED, one of the presentations was of a near-threshold flicker event (as in the previous experiments), the other was at a high frequency (100 Hz) that produces a fused percept, and participants were asked to report which of the two intervals contained the flicker. If the effect of perceptual load on flicker perception is indeed due to a change in sensitivity, accuracy and

d' scores for flicker detection should both be reduced under high (compared to low) perceptual load in the letter search.

3.4.2. Method

Participants: Eight new volunteers took part in the experiment. Their mean age was 25 (range 17-32), six were female and all were right-handed. All participants had normal or corrected-to-normal vision.

Critical flicker fusion threshold measurement: The CFF threshold was again measured for each participant individually at the beginning of the experimental session, using the method of constant stimuli. However, like the main experiment it now involved a 2IFC. Each trial consisted of two 200 ms flicker presentations (without the letter search array), separated by 300 ms. Of the two flicker presentations, one was at a frequency chosen from 6 different frequencies (26 to 36 Hz, in steps of 2 Hz). There were 120 trials in total, 20 for each frequency. On 10 of each frequency's trials flicker was presented in the first of the two displays and on 10 in the second. The other flicker presentation in each trial was at a frequency of 100 Hz, far above the human CFF threshold. A high frequency, rather than fused light, was used so that the total amount of illumination in each presentation would be the same. Order of trials was randomized. 600 ms after the offset of the second display, the question '1st or 2nd?' appeared on the screen above the LED, and remained until a response was given. Participants reported which of the two presentations they thought contained flicker by pressing the left arrow key for the first presentation and the

down arrow key for the second. An inter-trial interval of 1000 ms followed response.

Participants were told that the LED would always flicker on one of the two presentations, and that it would sometimes be hard to tell which of the two it was so they should guess if they were not sure. The data obtained were used to estimate the participant's threshold frequency. Unlike Experiments 6 and 7 (where the threshold was defined as the frequency at which the participant would be equally likely to categorize the stimulus as flickering or fused), here the threshold was defined as the frequency at which participants would make correct responses on 75% of trials (halfway between chance and perfect performance). The threshold frequency was rounded to the nearest whole number, which was then used to determine the frequencies displayed during the experiment (see below).

Stimuli, design and procedure: The stimuli were similar to those of Experiment 6. The design and procedure were similar to those of the previous experiments, but each trial now consisted of two stimulus presentations. Each presentation lasted 200 ms and the two displays were separated by 300 ms. Each of the displays contained a target letter (X or N). As in the previous experiments, a frequency 3Hz lower than the threshold found in CFF threshold measurement was designated as the threshold for the experiment, and frequencies 1 Hz lower and higher were also used. On one of the two stimulus presentations the LED flickered at one of these near-threshold frequencies. On the other display, the flicker frequency was 100 Hz, far above the CFF threshold (high-frequency flicker rather than fused light was used so that the total amount of illumination

would be equal in the two displays). The question 'Same or different letter?' appeared on the screen, above the LED, 500 ms after the second stimulus offset. Participants were instructed to report whether the target letters in the two displays were the same (both X or both N) by pressing the left arrow key, or different (X and N in either order) by pressing the down arrow. Once a response was given the question disappeared, and was replaced after 250 ms by the question 'Flicker 1st or 2nd?' Participants pressed the left or down arrow to report flicker on the first or second display, respectively. Once a response was given the question disappeared, and the next trial began after an inter-trial interval of 1000 ms (see **Figure 3.5**).

The experiment consisted of four blocks in an ABBA order (with A representing low and B high perceptual load, or vice versa). The load of the first block was counterbalanced across participants. Each block consisted of 144 trials, and participant-terminated breaks were given after every 72 trials. Each block contained all 144 combinations of letter-target identity (X or N) and location (six possible locations) on the first and second display. The threshold frequency, threshold minus 1 Hz and threshold plus 1 Hz were each used on 25% of the trials in each block. Catch trials (half with a frequency of threshold minus 12 Hz and half with a frequency of threshold plus 12 Hz, as in the previous experiments) were used in the remaining 25% of trials. As in the previous experiments, the catch trials were used to control for possible response biases and to make sure participants were attending to the task. The flicker occurred in the first presentation of the trial on half of each frequency's trials, and in the second on the other half. Trial order was randomized independently for the Letter search and flicker frequencies within each block. Participants performed two 72-

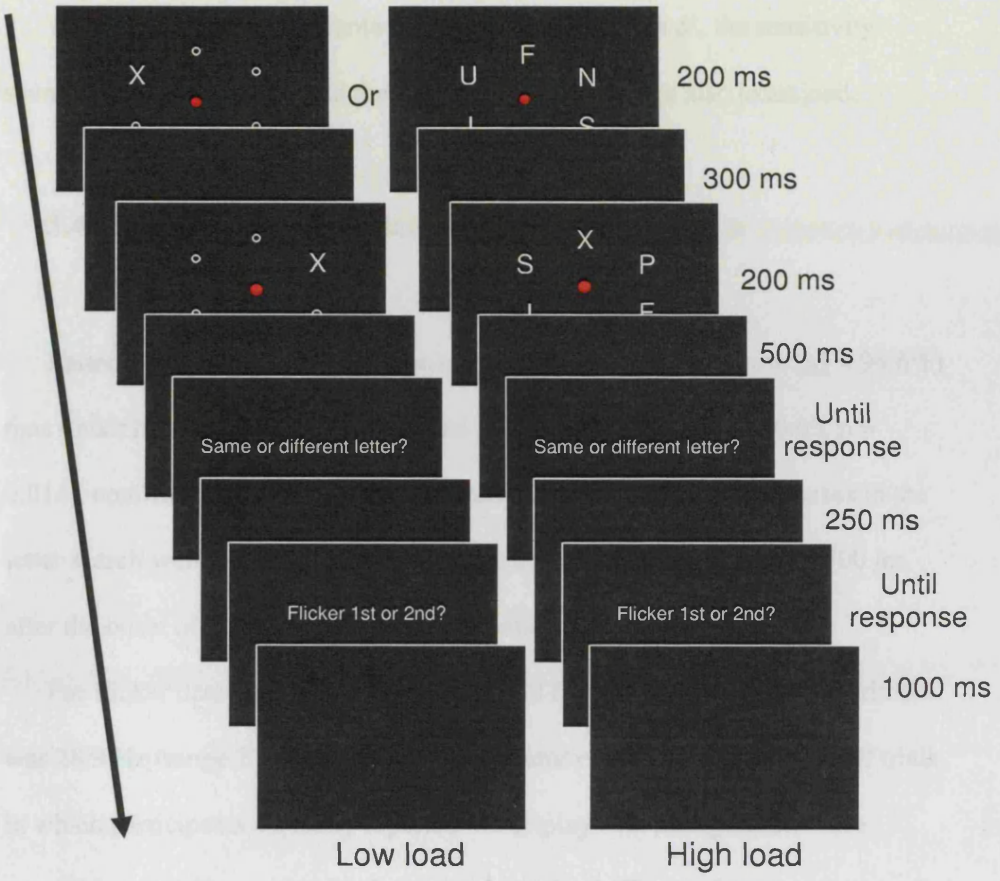

Figure 3.5. Experiment 8: Trial sequence. Following two consecutive displays of simultaneous letter and flicker stimuli, a question regarding the letter search appeared on the screen until a response was given. It was replaced by a question regarding the flicker, which also remained on the screen until response. Here, the answer to the letter question would be 'same' for the low-load example on the left, and 'different' for the high-load example on the right. The trial ended with a 1000 ms inter-trial interval. Figure not to scale.

trial blocks (one under each load condition) as practice before the experiment began. The entire experimental session lasted about two hours.

The main dependent variable for flicker detection was d', the sensitivity score[1], but accuracy rates and the criterion measure *c* were also examined.

3.4.3. Results and discussion

Letter search accuracy rates were significantly higher under low (M = 94.6%) than under high (M = 86.5%) perceptual load ($t_{(7)} = 2.767$, SEM = 0.03, p = 0.014), confirming that the load manipulation was effective. As responses in the letter search were delayed (participants could not give a response until 700 ms after the onset of the second display), RT data were not examined.

For flicker detection, the average threshold frequency used in the experiment was 28.9 Hz (range 27-31 Hz). To assess accuracy rates, the percentages of trials in which participants correctly reported the display containing flicker were entered into a 2 (Perceptual load: Low or high) by 3 (Flicker frequency: Threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated-measures ANOVA. There was a significant main effect of perceptual load ($F_{(1,7)} = 12.045$, MSE = $6.376*10^{-3}$, p = 0.01). There was also a marginally significant main effect of frequency ($F_{(2,14)} = 3.603$, MSE = $6.058*10^{-3}$, p = 0.055), and no interaction between load and frequency ($F_{(2,14)} = 1.472$, MSE = $3.604*10^{-3}$, *ns*). As

[1] This measure was calculated using the formula $d' = (1/\sqrt{2})[Z(H) - Z(F)]$, which is a modification of the standard formula $d' = Z(H) - Z(F)$ for 2IFC (or any other 2-alternative forced choice) paradigms. Z(H) stands for the Z-score associated with the probability of a Hit, and Z(F) for that associated with the probability of a False alarm. A hit was defined as a trial in which flicker was reported to have occurred in the first display, when it was indeed presented in the first display. A false alarm was defined as a trial in which flicker was again reported to have occurred on the first display, but was actually presented in the second display. Using reports of flicker on the second display would yield complementary probabilities and lead to the same d' values (Macmillan & Creelman, 1991).

predicted, the main effect of load was due to a reduction in accuracy under high perceptual load (M = 75.4% versus 67.1% under low and high load, respectively, when collapsed across all three frequencies; 80.2% versus 69.1% for threshold minus 1 Hz; 76.4% versus 67.5% for the threshold frequency; and 69.4% versus 65.4% for threshold plus 1 Hz).

d' scores were entered into a similar ANOVA as accuracy rates. There was a significant main effect of perceptual load ($F_{(1,7)} = 11.801$, MSE = 0.228, p = 0.011), showing a reduction in sensitivity under high perceptual load (see **Figure 3.6**). However, the main effect of frequency did not reach significance ($F_{(2,14)} = 2.172$, MSE = 0.188, *ns*), and nor did the interaction between load and frequency ($F_{(2,14)} = 2.232$, MSE = $6.459*10^{-2}$, *ns*).

As in the previous experiments, the results of the threshold plus 12 Hz catch trials show that participants were indeed at chance when the two presentations were rendered indistinguishable due to being above the CFF threshold, even though there was a difference of over 50 Hz between them (49.4 versus 52.1% for low and high load, respectively; $t_{(7)} = 1.045$, SEM = 0.03, *ns*). The results of the threshold minus 12 Hz frequency catch trials demonstrate that participants were capable of detecting flicker under both load conditions when the flicker was at a very low frequency, though here there was a trend toward flicker being less detectable under high load (95.7 versus 86.6% for low and high load, respectively; $t_{(7)} = 2.052$, SEM = 0.04, p = 0.079). This indicates that the effect of load might be powerful enough to affect flicker frequencies far below the threshold.

Finally, the criterion measure *c*, indicating the degree to which participants had a bias toward reporting the first or the second presentation as containing

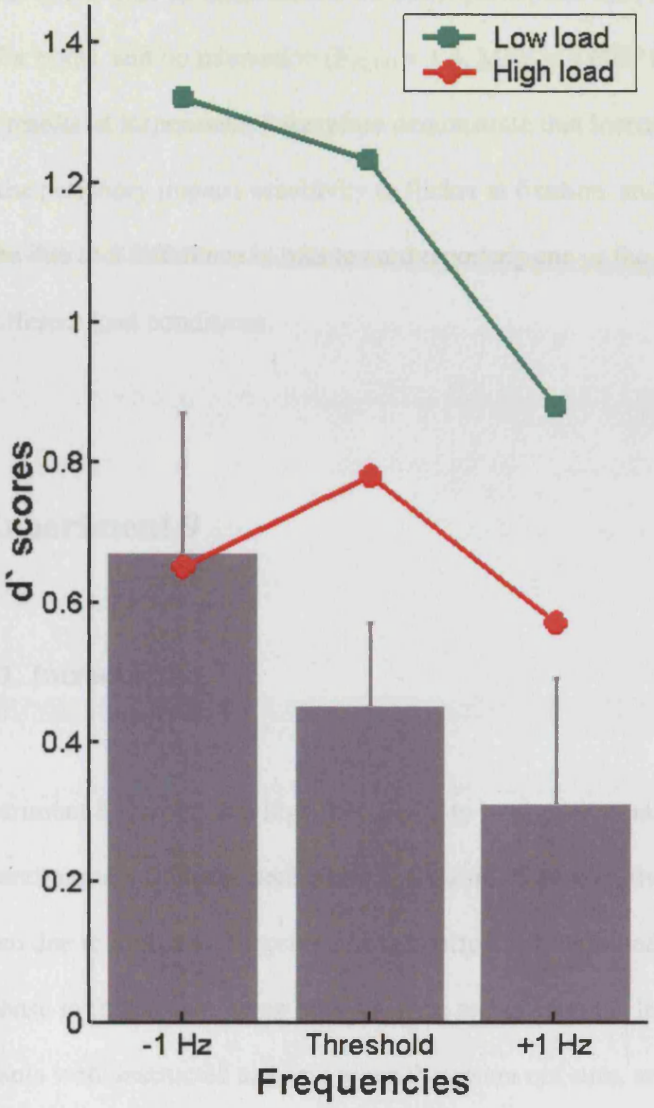

Figure 3.6. Experiment 8: Flicker detection results. Mean d' scores were lower under high (red circles) than under low (green squares) perceptual load. The grey bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

flicker, was entered into a similar ANOVA as the accuracy and sensitivity measures. There were no main effects for either perceptual load or frequency ($F < 1$, *ns* for both), and no interaction ($F_{(2,14)} = 1.4$, $\underline{MSE} = 4.608*10^{-2}$, *ns*).

The results of Experiment 8 therefore demonstrate that increasing perceptual load in the periphery impairs sensitivity to flicker at fixation, and that the effect cannot be due to a difference in bias toward reporting one or the other display under different load conditions.

3.5. Experiment 9

3.5.1. Introduction

Experiment 8 showed that high (compared to low) perceptual load in the letter search impaired flicker perception at fixation. However, this effect may have been due to increased forgetting of the correct response under high load, as the response to flicker was given only after the response to the letter search. Participants were instructed to guess when they were not sure, and could not continue the experiment until they had given a response. Therefore, if more forgetting occurred under high load, this would lead to a higher percentage of random responses (and lower accuracy rates and d' scores) under high than under low load.

In Experiment 9 this possibility was addressed by switching the order of the two responses. As responses to the flicker were collected first, 500 ms after the offset of the second display, any effect observed would be very unlikely to be

memory related. If the effect of perceptual load is indeed due to a loss of sensitivity under high load, it should be replicated here.

3.5.2. Method

Participants: Seven new volunteers participated in the experiment. One was excluded from the analysis, as his low performance on the letter search (68%) under high perceptual load meant an insufficient number of trials was collected. The remaining six participants had a mean age of 30.7 (range 21-66). Three were female and all were right-handed and had normal or corrected-to-normal vision.

Stimuli, design and procedure: These were identical to Experiment 8, except that the order of responses was switched, so that participants first reported which display contained flicker, and then whether the target letters in the two displays were the same or different.

3.5.3. Results and discussion

As in Experiment 8, accuracy rates in the letter search were significantly higher under low ($\underline{M}$ = 90.2%) than under high ($\underline{M}$ = 83.2%) perceptual load ($t_{(7)}$ = 3.24, $\underline{SEM}$ = 0.02, p = 0.011), indicating the load manipulation was again effective.

For flicker, the average threshold frequency used in the experiment was 29 Hz (range 26-32 Hz). As in Experiment 8, the percentages of trials in which participants correctly reported the display containing flicker were entered into a 2

(Perceptual load: Low or high) by 3 (Flicker frequency: Threshold minus 1 Hz, threshold, and threshold plus 1 Hz) repeated-measures ANOVA. There was a significant main effect of perceptual load ($F_{(1,5)} = 20.535$, $\underline{MSE} = 1.247*10^{-3}$, $p = 0.006$). There was also a significant main effect of frequency ($F_{(2,10)} = 25.521$, $\underline{MSE} = 1.472*10^{-3}$, $p < 0.001$), and no interaction between load and frequency ($F_{(2,10)} = 1.094$, $\underline{MSE} = 2.492*10^{-3}$, *ns*). As in Experiment 8, the main effect of load was due to a reduction in accuracy under high perceptual load ($\underline{M} = 76.2\%$ versus 71% under low and high load, respectively, when collapsed across all three frequencies; 82.5% versus 76.8% for threshold minus 1 Hz; 73.2% versus 71% for the threshold frequency; and 72.8% versus 64.7% for threshold plus 1 Hz). The data also show that the main effect of frequency was due to a monotonic decrease in accuracy as frequency increased.

d' scores were entered into a similar ANOVA as accuracy rates. There was a significant main effect of perceptual load ($F_{(1,5)} = 7.618$, $\underline{MSE} = 0.118$, $p = 0.04$). There was also a significant main effect of frequency ($F_{(2,10)} = 12.417$, $\underline{MSE} = 9.611*10^{-2}$, $p = 0.002$). There was no interaction between load and frequency ($F < 1$, *ns*). The main effect of load was again due to a reduction in sensitivity under high perceptual load (see **Figure 3.7**). As with accuracy rates, the data show that the main effect of frequency was due to a monotonic decrease in d' scores as frequency increased.

Catch trial results were similar to those of Experiment 8: For the threshold minus 12 Hz frequency catch trials, the results again show that participants were capable of detecting and reporting flicker, under both load conditions, when it was at a very low frequency (97 versus 91.7% for low and high load, respectively; there was no significant difference between load conditions, $t_{(5)} =$

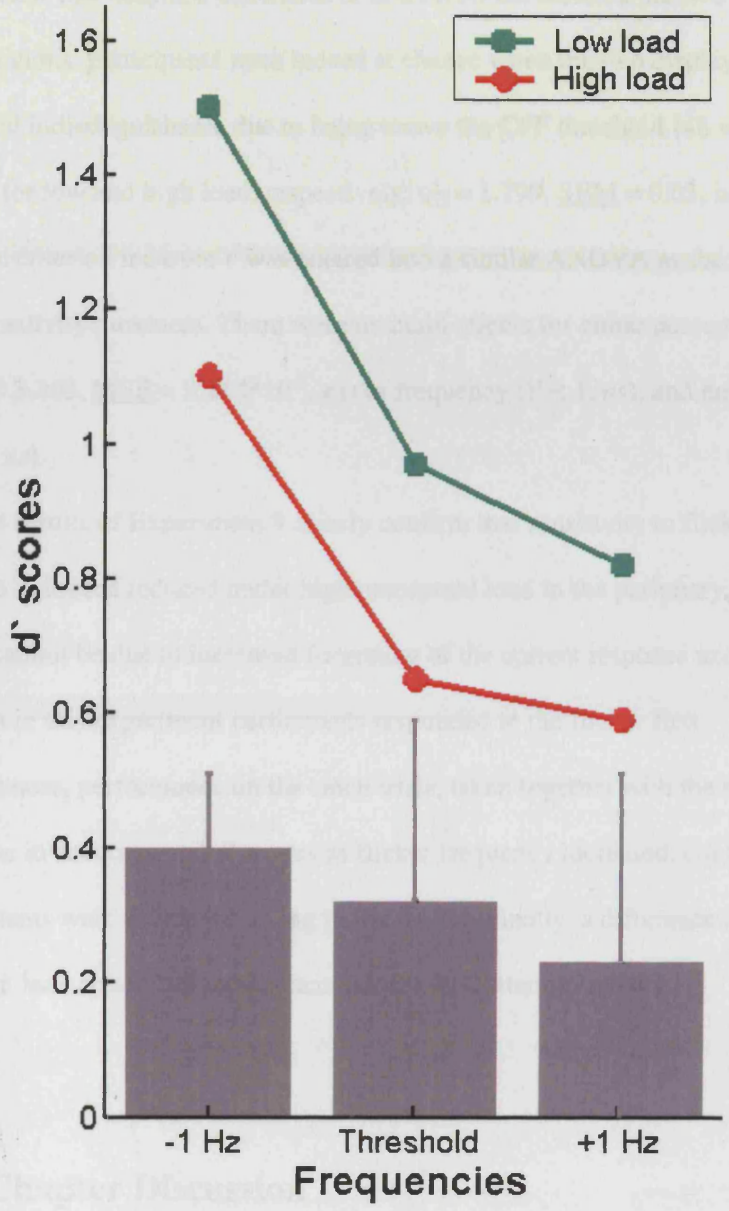

Figure 3.7. Experiment 9: Flicker detection results. As in Experiment 8, mean d' scores were lower under high (red circles) than under low (green squares) perceptual load. The grey bars represent the average differences between low and high perceptual load. Error bars represent 1 standard error of the mean.

1.528, SEM = 0.03, *ns*). For the threshold plus 12 Hz catch trials, the results again show that despite a difference of at least 50 Hz between the two presentations, participants were indeed at chance when the two displays were rendered indistinguishable due to being above the CFF threshold (48 versus 57.2% for low and high load, respectively; $t_{(7)} = 1.799$, SEM = 0.05, *ns*).

The criterion measure *c* was entered into a similar ANOVA as the accuracy and sensitivity measures. There were no main effects for either perceptual load ($F_{(1,5)} = 3.363$, MSE = $9.214*10^{-2}$, *ns*) or frequency ($F < 1$, *ns*), and no interaction ($F < 1$, *ns*).

The results of Experiment 9 clearly confirm that sensitivity to flicker at fixation is indeed reduced under high perceptual load in the periphery. This effect cannot be due to increased forgetting of the correct response under high load, as in this experiment participants responded to the flicker first. Furthermore, performance on the catch trials, taken together with the monotonic decrease in accuracy and d' scores as flicker frequency increased, confirms that participants were indeed attending to the flicker. Finally, a difference in bias between load conditions cannot account for the pattern of results.

3.6. Chapter Discussion

The central hypothesis of this study was that attention plays a role in visual awareness of temporal patterns. Specifically, it was predicted that in accordance with perceptual load theory (Lavie 1995, 2005), awareness of a visually-presented temporal pattern would depend on the amount of processing capacity

allotted to it. The results clearly show that perceptual load does indeed modulate flicker perception. Experiments 6 and 7 established that for the same flicker frequencies, increasing perceptual load in the periphery leads to reduced subjective awareness of flicker at fixation. The same flickering stimulus was more likely to be categorized as fused under high load in the peripheral letter search. This implies that subjective awareness of flicker depends on the availability of processing resources. In Experiments 8 and 9 the effect of perceptual load on sensitivity to flicker was established. The effect could not be due to either criterion differences between conditions, or to rapid forgetting of the correct response under high load.

Increasing perceptual load in a task that involved attention to shapes in specific spatial locations reduced the temporal resolution of visual awareness at fixation. This is in line with load theory (Lavie, 1995, 2005), which predicts that exhausting processing capacity will result in reduced awareness of unrelated stimuli. This chapter extends the findings of Chapter 2, showing that this is the case not only for awareness of spatial shapes, but also for temporal patterns. As load in a shape-related search impaired awareness in the temporal domain, the results of this chapter imply that general processing resources, directed by top-down attentional mechanisms, may be involved in various, and perhaps in all, aspects of visual awareness.

What are the neural mechanisms mediating awareness of temporal patterns, and its modulation by load? They are unlikely to be the same as the bottom-up mechanism for transient attention to peripheral locations proposed by Yeshurun and Levy (2003), whereby spatial cuing facilitates parvocellular activity and inhibits magnocellular activity in retinotopic areas corresponding to attended

locations. If top-down attention operated in a similar way, directing attention away from fixation (under high load) should have prevented magnocellular inhibition and thus *improved* flicker awareness. The fact that the opposite occurred indicates that top-down attention may involve different neural mechanisms. One possible candidate is the idea of a neuronal 'coalition' (Crick & Koch, 2003), involving a network of higher brain regions in frontal and parietal cortex, which has been associated with visual awareness in various experimental paradigms (Naghavi & Nyberg, 2005; Rees et al, 2002). The involvement of such a network in visual awareness of temporal patterns has never been investigated, and will therefore be the focus of the next chapter.

Chapter 4:

The involvement of frontal and parietal cortex in conscious awareness of flicker

4.1 Chapter Introduction[1]

In Chapter 3 I established the involvement of attention in temporal aspects of visual awareness, by showing that reducing the availability of attentional resources impairs the ability to perceive temporal patterns in vision. Awareness of temporal patterns is a fundamental aspect of conscious visual experience. However, the neural correlates of such temporally-dependent facets of awareness remain largely unknown. Recent studies show that visual awareness is associated not only with activity in occipital visual cortex but also in areas of frontal and parietal cortex (Naghavi & Nyberg, 2005; Rees, Kreiman, & Koch, 2002).

Neuroimaging research in healthy humans has shown that frontal and parietal activation is associated with the conscious detection of visual changes (Beck, Rees, Frith, & Lavie, 2001) and conscious word reading (Kjaer, Nowak, Kjaer, Lou, & Lou, 2001; Dehaene, Naccache, Cohen, Le Bihan, Mangin, et al, 2001), as well as the onset of stereo pop-out (Portas, Strange, Friston, Dolan, & Frith, 2000) and object identification (Eriksson, Larsson, Ahlstrom, & Nyberg, 2004). Such fronto-parietal activation is also time-locked to fluctuations in conscious perception during binocular rivalry (Lumer, Friston & Rees, 1998; Lumer & Rees, 1999) and other forms of bistable perception (Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998; Sterzer, Russ, Preibisch, & Kleinschmidt, 2002).

Similarly, lesions to parietal and frontal cortex can lead to deficits in awareness such as unilateral neglect, where patients typically fail to consciously perceive stimuli in one hemifield despite normal visual acuity (Driver &

[1] The research presented in this chapter has been published as: Carmel, D., Lavie, N., & Rees, G. (2006). Conscious awareness of flicker in humans involves frontal and parietal cortex. *Current Biology, 16*, 907-911.

Mattingley, 1998), and (at least partially) intact unconscious processing of such stimuli (e.g., Marshall & Halligan, 1988); and Balint's syndrome, where patients are only able to consciously perceive a single object at a time (e.g., Rizzo & Vecera, 2002). Furthermore, using Transcranial Magnetic Stimulation (TMS) to transiently disrupt frontal and parietal cortex activity in the healthy brain can impair conscious visual experience of changes in visual stimuli (Beck, Muggleton, Walsh, & Lavie, 2006; Turatto, Sandrini, & Miniussi, 2004).

The common involvement of these regions in diverse experimental paradigms suggests that they play a general role in visual awareness, and many studies have indeed suggested that attentional functions mediated by these regions are critical for awareness. However, it is not known whether activity in these areas is also associated with temporal aspects of subjective experience.

4.2 Experiment 10

In the current study I therefore used event-related functional Magnetic Resonance Imaging (fMRI) in humans to determine the neural correlates of conscious perception of flicker. As described in Chapter 3, the rapid luminance changes of flicker make it a good tool for studying temporal aspects of vision (Wells et al, 2001). Flicker at the CFF threshold, where a flickering light has an equal probability of being perceived as flickering or fused, constitutes a suitable stimulus for the study of awareness, as such threshold stimulation makes it possible to investigate different perceptual outcomes resulting from the same physical stimulus (Frith et al, 1999).

Despite the difference in the phenomenal quality of conscious perception at frequencies below and above the CFF threshold, neural activity corresponding to the frequency of a flickering stimulus has been observed in visual cortex at flicker frequencies as high as 90Hz, far exceeding the CFF threshold. Such observations were made using single-unit (Gur & Snodderly, 1997; Krolak-Salmon, Henaff, Tallon-Baudry, Yvert, Guenot, Vighetto, Mauguiere, & Bertrand, 2003), multi-unit (Rager & Singer, 1998) and EEG (Hermann, 2001; Lyskov, Ponomarev, Sandstrom, Mild, & Madvedev, 1998) recordings. Indeed, psychophysical work has shown that flicker above the CFF threshold can still lead to adaptation effects (Shady, MacLeod, & Fisher, 2004), and that the conscious experience of flicker arises following binocular fusion (Andrews et al, 1996). Flicker perception is therefore unlikely to be the property of neurons in early visual cortex; instead, it may result from the activity of neuronal 'coalitions' (e.g., Crick & Koch, 2003) operating at later stages of visual processing.

The evidence cited above implies that the CFF threshold is not the point where neurons in visual cortex can no longer match the temporal frequency of the stimulus, but rather the point where sensory registration and perceptual awareness are dissociated. Most previous neuroimaging studies of flicker have not attempted to compare activity related to the different subjective percepts evoked by flickering stimuli. Rather, they used PET (Fox & Raichle, 1984, 1985) or fMRI (Singh, Smith, & Greenlee, 2000; Hagenbeek, Rombouts, van Dijk, & Barkhof, 2002) to characterize the relationship between temporal frequency and evoked activation in visual cortex, employing frequencies above and below the CFF threshold and finding a peak of activation around 8 Hz, far below the

threshold. The only study that used fMRI to explicitly compare flickering and fused percepts (Zafiris, Kircheis, Rood, Boers, Haussinger, & Zilles, 2004) used frequencies below and above the threshold, respectively. In contrast, here it was possible to avoid confounding physical stimulation and perceptual outcome by characterizing brain activity associated with different conscious percepts (flickering or fused), but evoked by physically identical stimuli (flicker at the CFF threshold).

The consistent finding that neurons in early visual cortex can reflect frequencies far above the CFF threshold (Gur & Snodderly, 1997; Hermann, 2001; Krolak-Salmon et al, 2003; Rager & Singer, 1998; Lyskov et al, 1998; Shady et al, 2004) suggests that perception of flicker at threshold frequencies may depend instead on activity in higher cortical regions. Specifically, fluctuations of attention-related activity in these higher-level regions might determine whether the same stimulus will lead to a flicker or fused percept. The hypothesis I examined here was therefore that the frontal and parietal regions known to mediate attention and previously implicated in non-temporal aspects of awareness (see Naghavi & Nyberg, 2005; Rees et al, 2002 for reviews) would also be involved in conscious awareness of flicker.

4.3 Method

Participants: Thirteen healthy volunteers (11 female, mean age 26.4, range 23-34) gave written informed consent to participate in the study. All participants had normal or corrected to normal vision.

fMRI scanning parameters: A 3T Siemens Allegra system was used to acquire both T1 weighted anatomical images and T2-weighted echoplanar (EPI) images with Blood Oxygenation Level Dependent (BOLD) contrast. Each EPI image comprised forty 3 mm axial slices with an in-plane resolution of 3x3 mm positioned to cover the whole brain. Participants performed between two and four runs, each consisting of 276 volumes. The first six volumes of each run were discarded to allow for T1 equilibration effects. Volumes were acquired continuously with a TR of 2.6 s per volume.

Stimuli and apparatus: Participants lay supine in the MRI scanner. On each trial, they fixated a single red LED (CIE chromaticity coordinates x=0.655, y=0.344), placed at the centre of the head end of the scanner bore, approximately 70 cm from the participants' head. The LED was viewed through a mirror mounted on the head coil and subtended 0.3° visual angle. On each trial, the LED flickered for 500 ms (square-wave flicker, 1:1 duty cycle; luminance 29 cd/m^2 at 30 Hz). The foveal presentation and brief duration minimized temporal adaptation effects (Curran & Wattis, 1998). To aid fixation, four fluorescent nonius lines (at right angles to each other in a '+' configuration) were placed around the LED. The room was completely dark apart from the LED and nonius lines. On each trial, participants reported by button press whether they perceived the light as flickering or not.

Behavioural threshold measurement: To observe the neural correlates of the percept (flickering or fused) while keeping the physical stimulus constant, the CFF threshold (the frequency at which a flickering light has an equal probability

of being perceived as flickering or fused) was first assessed for each participant individually. The threshold was assessed at the beginning of the experimental session, in the scanner (but prior to scanning), using the procedure described in **Section 3.2.2**. The only differences to the assessment procedure used in the behavioural experiments of Chapter 3 were that the duration of each flicker event was 500 (rather than 200) ms, and responses were given using an MR-compatible response box (rather than a standard keyboard).

fMRI scanning procedure: As in Chapter 3, three frequencies were used in the experimental conditions in order to eliminate the tendency to adopt a constant response if only a single stimulus were to be used repeatedly: The pre-assessed threshold (rounded to the nearest whole number), and frequencies 1 Hz lower and 1 Hz higher. Null events, in which no stimulus appeared, were also included. There were an equal number of threshold frequency, threshold minus 1 Hz, threshold plus 1 Hz and null event trials. In addition, to further monitor for any response bias, each scanner run contained a small number of catch trials in which the frequency was reliably above or below CFF threshold; either 8 Hz higher (5% of trials) or 8 Hz lower (5% of trials).

During each scanner run participants were presented with 120 trials. Stimuli belonging to different conditions (threshold, threshold ± 1 Hz, catch trials and null events) appeared in random order. Each flicker event lasted 500 ms with a stimulus onset asynchrony of 5.85 s. Similar to the threshold assessment, participants reported their percept (flicker or fused) by pressing a response box key. Participants were informed that the LED would sometimes flicker, but were

not told that they would be presented with different frequencies, that the same frequency may lead to different percepts, or that there would be catch trials.

Data analysis: Responses were recorded on each trial. If the participant made more than one key press, gave no response (except on null-event trials, where that was the correct response), or responded within less than 150 ms from stimulus onset, the trial was excluded and not used as one of the 'flicker' or 'fused' trials in the subsequent fMRI analysis.

Functional imaging data were analyzed using Statistical Parametric Mapping software (SPM2, Wellcome Department of Imaging Neuroscience, UCL). All image volumes were realigned to the first, and temporally corrected for slice acquisition time (using the middle slice as reference). Resulting volumes were spatially normalized to a standard EPI template volume based on the MNI reference brain in the space of Talairach and Tournoux (1988). Normalized image volumes were smoothed with an isotropic 6mm FWHM Gaussian kernel.

An event-related random-effects model was used for statistical analysis. For each participant, voxels activated in the experimental conditions were identified using a statistical model which contained regressors representing the transient responses evoked by individual trials in each condition. The event-related changes in evoked activity were modelled by convolving a synthetic haemodynamic impulse response function with trains of unitary events corresponding to trial onsets. Each component of the model served as a regressor in a multiple regression analysis that included all nine experimental conditions (three frequencies by two possible percepts, plus two types of catch trial, and null events), as well as motion correction parameters (as effects of no interest). The

data were high-pass filtered (cut-off frequency 0.0078 Hz) to remove low-frequency signal drifts. Global changes in activity were removed by proportional scaling, and the data were corrected for temporal auto-correlations. For each voxel, the resulting parameter estimates for the six conditions of interest (threshold frequency, 1 Hz below threshold and 1 Hz above threshold with two perceptual outcomes – flicker or fused – for each) were then entered into a second level analysis where each participant served as a random effect in a within-subjects ANOVA. The main effects of percept (flicker or fused) and frequency (threshold – 1 Hz, threshold, threshold + 1 Hz) and any interaction between these factors were specified by appropriately weighted linear contrasts on a voxel-by-voxel basis.

Eye position monitoring: During scanning, eye position was continually sampled at 60Hz using long-range infrared video-oculography (ASL 504LRO Eye Tracking System, Mass). The measures recorded were x and y coordinates of gaze direction (later combined to calculate the distance of fixation from the LED the participants were instructed to fixate on), and pupil diameter. Data were initially preprocessed to temporally detrend the signal and remove blinks. The average distance of fixation from the LED and the average pupil diameter were then computed for each 500 ms trial. In order to see whether eye-position or pupil diameter differed systematically between the flicker and fused conditions, the mean distance from fixation and the pupil diameter in each condition were subjected to a two-tailed paired t-test. A similar test was also performed on the standard deviations of the distance from fixation in each condition, to see whether either percept (flicker or fused) was associated with greater variance in

eye-position. The low temporal (60Hz) and spatial (~0.25° degrees) resolution of the eye-tracker, and the relatively low signal-to-noise ratio (due to the distance of the infra-red illuminant and optics from the eye), all currently necessitated by long-range eye tracking in scanning environments, precluded any formal assessment of fixational eye movements (microsaccades, drifts and tremor).

4.4 Results

Behaviour: Mean flicker fusion threshold was 29.85 Hz across participants (range 24Hz - 35Hz). Flicker percepts were reported on 41% of trials (range 29%-66%), so there were large numbers of both flicker and fused percepts for all participants. Performance on catch trials was nearly perfect, with a mean of 0.43 mis-categorizations (range 0-3) per 12 catch trials in each fMRI run. Participants were therefore attending to the task rather than responding in a random manner.

fMRI: A within-subject random effects ANOVA was used to reveal brain areas associated with effects of percept (flicker or fused), frequency (threshold minus 1 HZ, threshold, and threshold plus 1 Hz) and their interaction. In voxels where there was a significant effect of percept, t-tests were used to determine its direction. Physically identical trials evoking flicker (versus fused) percepts were associated with greater activation in predicted parietal and frontal regions (**Figure 4.1** and **Table 4.1**) e.g. intraparietal sulcus (Brodmann area 7, BA7), the inferior parietal lobule (BA40), the inferior (BA44), middle (BA46) and medial (BA6) frontal gyri, the anterior insula and the cingulate sulcus (BA32).

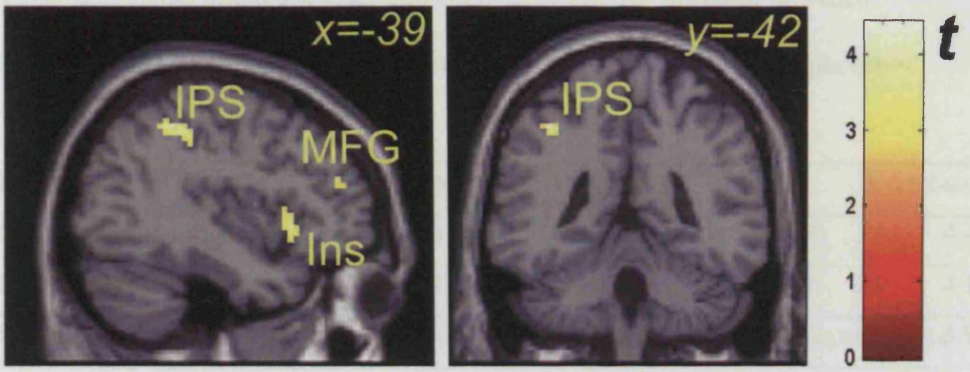

Figure 4.1. Experiment 10: Flicker > Fused. A number of the frontal and parietal areas where event-related activity was greater for flicker than for fused percepts are superimposed on sagittal and coronal sections of a T1-weighted anatomical template image in MNI space. All peaks of activation reaching statistical significance are listed in **Table 4.1**. A statistical threshold of Z = 2.58 (corresponding to $p<0.005$, uncorrected) and a cluster-size threshold of at least 10 voxels was used for display purposes in this and the following image. The MNI coordinate corresponding to the section's plane is indicated on each section. IPS: intraparietal sulcus, MFG: middle frontal gyrus, Ins: insula.

Activation was bilateral in frontal regions, but lateralized to the left in the parietal lobe.

In contrast, fused percepts were associated with activation in several brain regions (**Table 4.2** and **Figure 4.2**), especially occipital extrastriate cortex. Activation was bilateral, but the most significant activations were observed in the right hemisphere. No brain areas showed a significant main effect of frequency or an interaction between frequency and percept. The absence of any interaction rules out the possibility that the differential brain activity associated with different percepts, described above, could be due to the different frequencies used. It is conceivable, for example, that the contrast flicker > fused would reflect an effect mostly present for the threshold – 1 Hz frequency, and that the

Table 4.1. Experiment 10: Loci and t-scores of cluster maxima in which there was significantly higher activation for flicker than for fused percepts

Region	Brodmann area	Hemisphere	x	y	z	t-score
Inferior parietal lobule	40	L	-57	-30	39	4.42
Inferior frontal gyrus	44	L	-60	9	21	4.11
Intraparietal sulcus	7	L	-39	-42	48	3.94
Middle frontal gyrus	46	L	-45	45	18	3.80
	46	R	48	48	9	3.57
Anterior insula	-	R	30	24	0	3.75
	-	L	-39	18	-3	3.61
Cingulate sulcus	32	L	-6	30	30	3.75
Medial frontal gyrus	6	L	-12	-6	57	3.59
Parieto-occipital fisure	7	L	-12	-75	45	3.55
Superior frontal gyrus	6	R	21	-18	66	3.48

Shown are significantly activated voxels in frontal and parietal cortex, at a threshold of $p < 0.001$, uncorrected (because of the prior hypothesis regarding these areas). Even at this uncorrected threshold, all activated loci fell within regions previously associated with visual awareness (Naghavi & Nyberg, 2005). Coordinates in this and the next table are given in standard MNI space. R: right hemisphere; L: left hemisphere.

contrast fused > flicker would reflect an effect mostly present for the Threshold + 1 Hz frequency. However, this would lead to a significant interaction of frequency and percept in the voxels where the main effect of percept was found. Furthermore, an observation of the effects in activated regions, as **Figure 4.3** illustrates, shows that there was no significant or consistent effect of frequency.

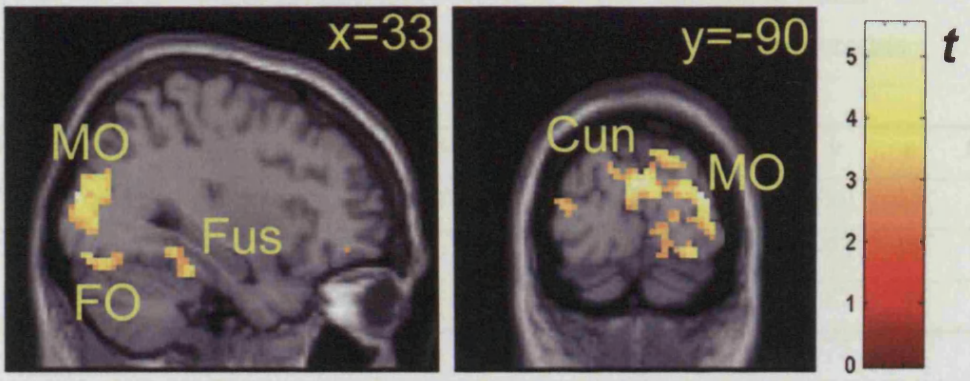

Figure 4.2. Experiment 10: Fused > Flicker. Sagittal and coronal sections of a T1-weighted anatomical template image in MNI space, with superimposed areas where event-related activity was greater for fused than for flicker percepts. Most of this activity occurred in occipital extrastriate regions. The full list of activation peaks reaching statistical significance is given in **Table 4.2**. MO: middle occipital gyrus, FO: fourth occipital gyrus, Fus: fusiform gyrus, Cun: cuneus.

Eye monitoring: Eye monitoring data were available for eight of the thirteen participants, and showed no significant differences between flicker and fused percepts for either mean distance from fixation ($t_{(7)} = 0.832$, SEM = 1.29, *ns*) or the standard deviation of distances ($t_{(7)} = 1.224$, SEM = 3.27, *ns*). This rules out any effect of saccades or variance in eye position on the neuroimaging findings, but it remains possible that microsaccades or other fixational eye movements could contribute to these findings.

In contrast to the distance measures, pupil diameter was significantly greater on flicker (versus fused) trials ($t_{(7)} = 4.217$, SEM = 0.23, $p = 0.004$). However, this effect was extremely small (a difference of ~0.05 mm, representing a change of ~2% in pupil area) and thus unlikely to result in differential activation in

Table 4.2. Experiment 10: Loci and t-scores of cluster maxima in which there was significantly higher activation for fused than for flicker percepts

Region	Brodmann area	Hemisphere	x	y	z	t-score
Middle occipital gyrus	18/19	R	33	-90	15	5.52
Cuneus	18/19	R	9	-93	18	5.19
	19	R	12	-87	36	4.33
Lateral occipital sulcus	18/19	R	42	-75	3	4.96
Fusiform gyrus	37	L	-36	-42	-15	4.83
Inferior frontal gyrus	45	R	54	30	12	4.61
Middle temporal gyrus	21	L	-57	-33	0	4.56
	21	L	-66	-27	-3	4.04
Cerebellum, posterior lobe	-	L	-24	-66	-21	4.56
Anterior occipital sulcus	18/19	L	-30	-75	-6	4.46
Postcentral gyrus	1	L	-39	-21	42	4.32
Insula	-	L	-30	6	18	4.24
Posterior transverse collateral sulcus	18/19	L	-21	-72	-6	4.46
Superior occipital gyrus	18/19	R	15	-102	6	4.15
Inferior occipital gyrus	18/19	R	30	-87	-15	4.14
	18/19	R	18	-99	-6	4.10
Transverse occipital sulcus	18/19	R	30	-81	18	4.07
	18/19	R	30	-84	9	4.04
	18/19	R	39	-75	21	3.98
Cerebellum (vermis)	-		0	-63	-3	4.05

As no prior hypothesis was defined regarding areas that would be activated when participants failed to detect flicker, a corrected threshold of $p < 0.05$ (FDR-correction) was used for this contrast, as well as for the main effect of frequency and the interaction of frequency and percept, for which no significant activations were found (see main text). R: right hemisphere; L: left hemisphere.

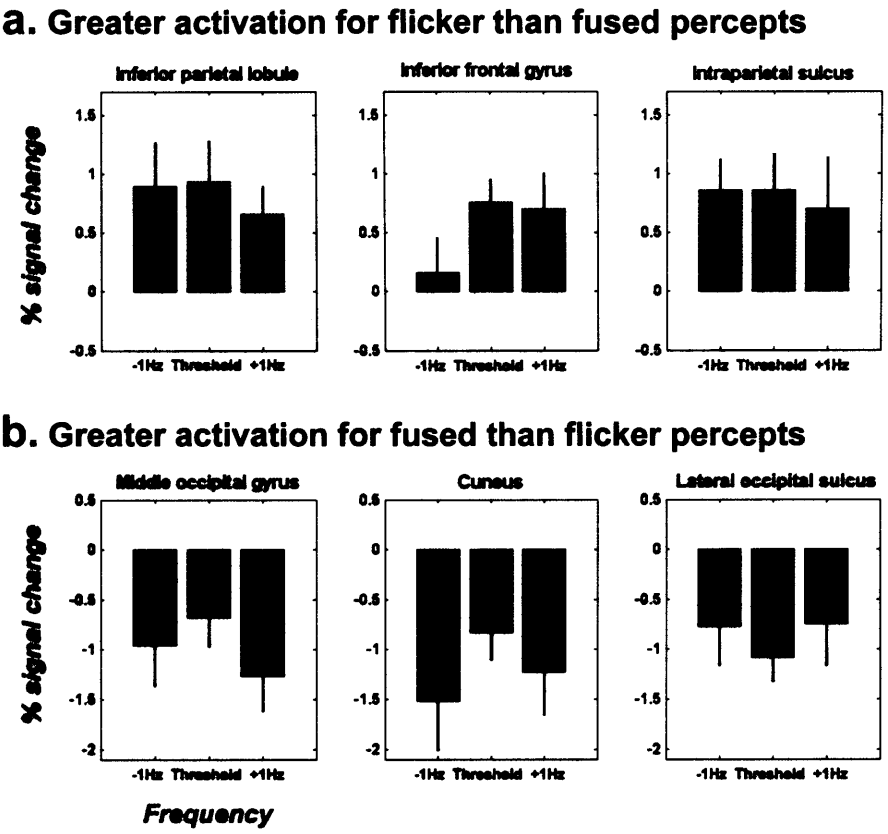

Figure 4.3. Experiment 10: Differences between the BOLD signals associated with flicker and fused percepts are similar for all three frequencies. BOLD signal change (percent difference) comparing flicker and fused percepts, for the three stimulus frequencies, averaged across the thirteen participants. For each panel, the y-axis shows the signal change for flicker minus signal change for fused; the x-axis shows the three frequencies (1 Hz below threshold, threshold, and 1 Hz above threshold). **(a)** the most significantly activated cluster maxima in the flicker > fused contrast; the subtraction should lead to positive values. **(b)** the most significantly activated voxels in the fused > flicker contrast; the subtraction should lead to negative values. As this figure illustrates, this is generally the case. This figure illustrates that there are no consistent trends or significant differences between the effects of percepts (flicker or fused) at different frequencies. Error bars represent 1 standard error of the mean.

visual cortex. Indeed, activation in extrastriate cortex was lower, not higher, on trials in which flicker was perceived despite pupil diameter being slightly larger (**Table 4.2**). Importantly, the difference in pupil diameter was apparent from trial

onset and remained similar in magnitude throughout the trial (as indicated by the first pupil diameter measurement in a trial: $t_{(7)}$=4.667, SEM = 0.21, p=0.002; and also by dividing the trial into 100-ms bins: flicker > fused in all bins, main effect of flicker versus fused $F_{(1,7)}$=18.28, MSE = 1.014, p=0.004; all $t_{(7)}$ scores for the separate bins > 4.166, p = 0.004; no interaction between bin and percept, F < 1, *ns*).

4.5 Discussion

Flickering and fused percepts were associated with distinct patterns of activation in response to physically identical flickering stimuli. Specifically, perception of flicker was associated with greater activation in bilateral frontal and left parietal cortex. This cortical network has previously been associated with awareness in tasks that did not specifically examine the temporal aspects of subjective experience in a non-spatial task, as studied here (Beck et al, 2001, 2006; Dehaene et al, 2001; Driver & Mattingley, 1998; Eriksson et al, 2004; Kjaer et al, 2001; Kleinschmidt et al, 1998; Lumer et al, 1998; Lumer & Rees, 1999; Naghavi & Nyberg, 2005; Portas et al, 2000; Rees et al, 2002; Rizzo & Vecera, 2002; Sterzer et al, 2002; Turatto et al, 2004). These new findings demonstrate that this network is also involved in awareness of temporal non-spatial properties of the visual environment, and may therefore play a general role in visual awareness.

Patients with right parietal damage are impaired in temporal discrimination (distinguishing flicker onsets from offsets), but have no impairment in flicker

detection (Battelli, Cavanagh, Martini, & Barton, 2003). This is consistent with the current finding of left parietal activation for flicker detection. Taken together, these findings suggest that right parietal damage may be associated with the disruption of an attentional process devoted to relative timing (Battelli et al, 2003) but not with the detection of temporal patterns, which may be functionally preserved in the intact left parietal lobe.

Neurons in visual cortex represent flicker at much higher frequencies than the CFF threshold (Gur & Snodderly, 1997; Hermann, 2001; Krolak-Salmon et al, 2003; Rager & Singer, 1998; Lyskov et al, 1998; Shady et al, 2004), consistent with the finding that there was no interaction of frequency and percept (**Figure 4.3**). Fronto-parietal activity related to the percept of flicker may thus be associated with processes linked to awareness rather than sensory processing per se. The present findings are also consistent with theories of visual awareness in which awareness is constrained not by the properties of early visual neurons, but rather by a higher-level network comprising neuronal 'coalitions' or serving as a 'global neuronal workspace'. In such views, consciousness arises from the interaction of widespread networks across the brain, rather than from activity in early sensory cortex (Baars, 2002; Crick & Koch, 2003; Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001).

As a single point source of light was used in this study, shifts of spatial attention cannot account for these findings (unlike many previous studies of visual awareness: Beck et al, 2001, 2006; Dehaene et al, 2001; Driver & Mattingley, 1998; Eriksson et al, 2004; Kjaer et al, 2001; Kleinschmidt et al, 1998; Lumer et al, 1998; Lumer & Rees, 1999; Portas et al, 2000; Rizzo & Vecera, 2002; Sterzer et al, 2002; Turatto et al, 2004). However, the data also

raise the intriguing and rather different possibility that non-spatial attention, known to be associated with similar fronto-parietal activation as found here (Wojciulik & Kanwisher, 1999) is involved in conscious flicker perception. Functional imaging data cannot determine whether fronto-parietal activation plays a causal role in flicker detection, or whether it results from such detection. For example, perceived flicker may attract attention automatically due to the sharp luminance onsets, and fronto-parietal activity may reflect this. Alternatively, flicker detection may be facilitated when activity levels in fronto-parietal cortex are high, consistent with a causal role for (non-spatial) attentional functions of frontoparietal cortex in flicker awareness.

Interestingly, the latter possibility is supported by the current finding that flicker percepts were associated with a slightly larger pupil diameter from trial onset. Pupil dilation has previously been associated with attention and effort (Kahneman, 1973) and pupil dilation induced by task difficulty has been associated with activity in frontal and parietal regions (Siegle, Steinhauer, Stenger, Konecky, & Carter, 2003). Speculatively, it is possible that the difference in pupil size observed here may therefore result from cortical activity related to attentional effort in the flicker detection task, reflecting a pre-existing brain state that may have determined the perceptual outcome of each trial. Attentional effort may have fluctuated between trials, with increases in attention leading both to better flicker detection and to pupil dilation. Importantly, attention would not be directed at spatial, but rather at temporal properties of the stimulus.

Such a notion receives support from recent behavioural work showing that temporal parsing of visual input is sensitive to attentional manipulation (Carrasco

& McElree, 2001; VanRullen et al, 2005; Visser & Enns, 2001; and the results reported in Chapter 3 of this thesis). The fronto-parietal activity found here may reflect a general role of attention in enhancing the detection and selection of any target event (be it temporal or spatial), but it is important to note that since participants reported their percept on both flicker and fused trials, the ability to report the target cannot, in itself, account for observations of fronto-parietal activity associated with flicker perception.

In contrast to conscious perception of flicker, fused percepts were predominantly associated with activation of occipital cortex. The foveal presentation of the flicker stimulus and the random-effects analysis (which necessarily averaged across participants) do not permit determination of the precise retinotopic location of these activations. However, they fall clearly outside the calcarine sulcus and therefore are likely to reflect activity in extrastriate visual cortex (Dougherty, Koch, Brewer, Fischer, Modersitzki, & Wandell, 2003). The finding of activated extrastriate foci for physically identical (though perceptually distinct) stimuli is surprising but clearly rules out the possibility that successful flicker detection relies on activity in early visual cortex (either instead of or in addition to the fronto-parietal activity). It is well established that activity in visual cortex can more closely reflect phenomenal experience than physical stimulation (Ress & Heeger, 2003; Tong, 2003). The present findings suggest that such differences in activity of visual cortex may extend to situations where phenomenally different experience arises from different temporal parsing of visual input.

To conclude, frontal and parietal cortical regions were involved in detecting flicker in a single, small point source of light. As activity in similar cortical areas

has previously been associated with visual awareness in a variety of other tasks that have not involved detection of a temporal pattern, these findings suggest that frontal and parietal cortex may play an important general role in supporting visual awareness.

Chapter 5:

Working memory maintains perceptual biases during binocular rivalry

5.1 Chapter Introduction

Chapters 2 and 3 established the role of perceptual load in visual awareness in presence/absence detection (Chapter 2) and temporal patterns (Chapter 3). In the present chapter I turn to examine the role that the active executive control mechanism postulated by load theory (Lavie, 2000; 2005; Lavie et al, 2004) plays in visual awareness. Load theory proposes that working memory maintains prioritization of current stimulus preferences, enabling the rejection of irrelevant distractors. In other words, working memory is required to maintain biases in the allocation of processing resources, in situations where stimuli compete for them (see **Section 1.3.1**).

Until recently there had been little direct behavioural evidence in healthy humans for the causal role of working memory in the top-down control of biased visual competition (Desimone & Duncan, 1995). In a series of studies, however, Lavie and colleagues demonstrated that reducing the availability of working memory by loading it in a concurrent unrelated task results in reduced ability to maintain task priorities, and greater interference from irrelevant distractors. High (compared to low) working memory load increased behavioural interference from irrelevant distractors in flanker tasks (Lavie et al, 2004), and Stroop-like tasks (De Fockert et al, 2001), as well as increasing interference from irrelevant, but salient distractors in attentional capture (Lavie & De Fockert, 2005). Additionally, a neuroimaging study showed that brain activity associated with ignored faces increased under high working memory load (De Fockert et al, 2001; for a full review of these studies, see **Section 1.3.3**). Similar effects of working memory load, however, were not found for visual search (Logan, 1978;

Woodman et al, 2001), suggesting that the deciding factor in whether or not working memory load will increase interference is not simply the presence of irrelevant stimuli, but competition between salient stimuli.

Does the role of executive processes in stimulus selection generalize to visual awareness as well? If working memory is indeed needed to act as a top-down control mechanism, biasing perception in all situations that involve visual competition among salient stimuli, then a specific task defining the behaviourally-relevant targets may not be necessary. If this is the case, then loading working memory should have an effect on the competition in binocular rivalry, a fundamental form of visual competition that occurs in the absence of an explicit attentional task. Specifically, loading working memory should reduce the visual system's ability to maintain a stable and coherent percept in binocular rivalry.

As binocular rivalry is investigated in this and the next chapter, I will now briefly review the studies on binocular rivalry that set the context for the present studies.

5.2 Binocular rivalry

Binocular rivalry occurs when sufficiently dissimilar images are presented to corresponding retinal areas of each eye. Instead of a coherent, fused image being perceived, what normally transpires (after a brief period during which both images are perceived) is a pattern of shifts in perceptual dominance, with one image perceived at any given time and the other image suppressed (**Figure 5.1**).

Changes in dominance typically occur quickly but not immediately, so brief periods of mixed percept are also experienced. Dominance alternates between the two images, with dominance phases typically lasting a few seconds. Though it has been claimed that practice can improve the ability to control shifts intentionally, this seems to be very difficult (Meng & Tong, 2004), and normally the length of dominance phases appears to be random. Like many other stochastic phenomena (such as alternations of perception for the Necker cube or the Rubin face-vase), the frequency histogram of phase-lengths closely resembles a mathematical function known as a gamma distribution (**Figure 5.2**, Blake, 2001; Blake & Logothetis 2002).

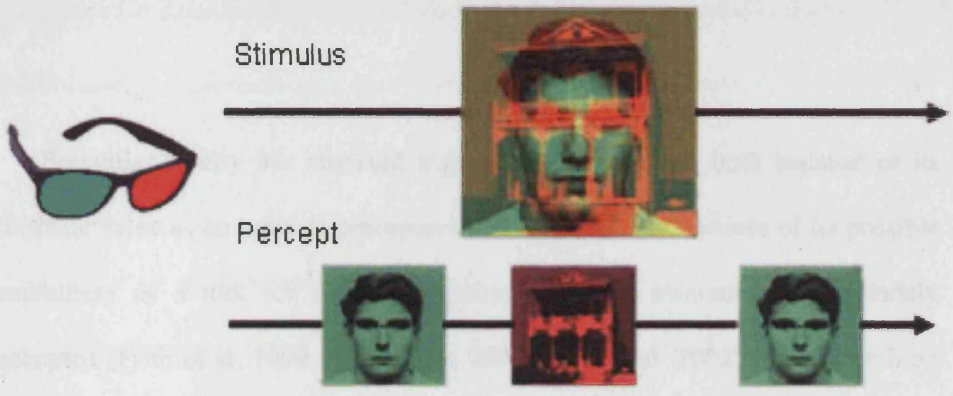

Figure 5.1. An example of binocular rivalry. When viewed through anaglyph red-green goggles (shown left), the image containing a superimposed red house and green face (top) induces binocular rivalry, leading to an alternating pattern of perceptual dominance (bottom). From Tong et al (1998).

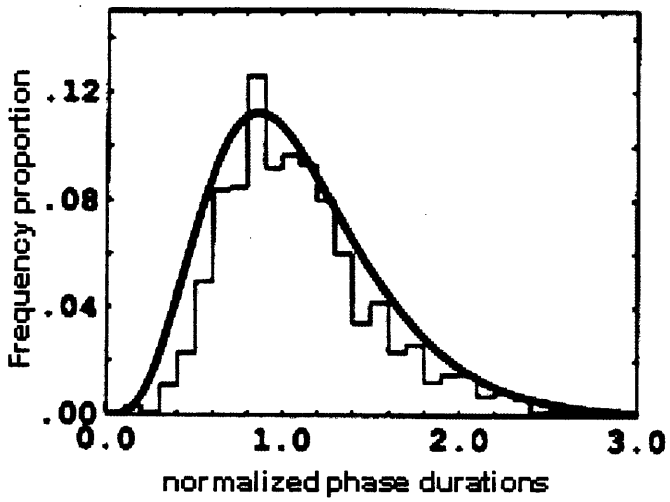

Figure 5.2. A histogram summarizing the durations of individual dominance phases during binocular rivalry. Observers reported their percepts by pressing one of two keys, and the individual durations were tabulated (put into fixed-width bins), normalized (each value was divided by the mean) and plotted as a frequency histogram. The solid line shows the gamma function fit to the actual data. From Kovacs et al (1996).

Binocular rivalry has attracted a great deal of interest, both because of its intrinsic value as an unusual perceptual phenomenon, and because of its possible usefulness as a tool for the investigation of visual awareness: It is widely accepted (Frith et al, 1999; Kanwisher, 2001; Rees et al, 2002) that research on awareness can benefit from the use of procedures in which physical stimulation is held constant while conscious experience changes, and binocular rivalry is a classic example of constant retinal input bringing about changes in subjective experience (Blake & Logothetis, 2002; Tong, 2001).

5.2.1 The neural locus of binocular rivalry

One of the major debates in the binocular rivalry literature concerns the locus of the competition: Does it take place 'early' (between monocular neurons in primary visual cortex or even the lateral geniculate nucleus) or 'late' (between representations in areas further along the visual stream). The new research presented in this chapter is not directly related to this debate, but does inform the discussion of whether rivalry should be viewed as a low-level perceptual phenomenon, or as a complex one involving several processing levels. As a great deal of what is known about rivalry was found in the context of the early-late debate, I shall briefly review the current literature. I will show that while there is evidence to support both possibilities, the terms of the debate may be oversimplified and a more refined view of rivalry may be required to fully understand it.

Behaviourally, it has been shown that when written words and line drawings are presented within the suppressed image, they are not processed semantically (not even at an implicit level), indicating an early locus of suppression (Blake, Ahlstrom, & Alais, 1999; Cave, Blake, & McNamara, 1998; Zimba & Blake, 1983). On the other hand, motion after-effects elicited by motion presented to one eye reach their full magnitude even if they are rivalrously suppressed part of the time (Lehmkuhle & Fox, 1975; O'shea & Crassini, 1981), and motion presented within the suppressed image can bias the perception of motion in the dominant image (Andrews & Blakemore, 1999, 2002; Blake et al, 1999). This seems consistent with late suppression (at least as late as the motion-sensitive area V5/MT+), but could also indicate that various visual pathways are

differentially effected by rivalry. Such a view is corroborated by fMRI findings that emotional faces, suppressed in rivalry, can still lead to activation in regions of the limbic system (e.g. the amygdala), which are known to be involved in emotional processing (Williams, Morris, McGlone, Abbott, & Mattingley, 2004; Pasley, Mayes, & Schultz, 2004). Both motion and emotion information are known to be processed by the tectopulvinar system, which contains pathways leading from the optic tract, via the superior colliculi, to the pulvinar and further to stimulus-specific regions (Pasley et al, 2004). Such information may therefore be fully processed in an 'alternative route' even if rivalry suppression occurs early in the geniculastriate pathway (e.g. in V1).

Furthermore, the possibility that representations of the suppressed image exist in 'late' parts of the ventral visual system is supported by behavioural evidence showing that interocular grouping can take place between the two images, allowing rivalry to occur between coherent representations constructed from *parts* of the rivalling images, and therefore indicating that rivalry occurs beyond the point where information from the eyes is combined (Kovacs, Papathomas, Ming, & Feher, 1996). Also, when the two images are rapidly switched between the eyes (so that each eye sees a rapid succession of the two images but the two eyes see a different image at any time), perceptual alternations can exhibit the same temporal dynamics as when static patterns are used: a single dominance phase may span multiple eye-alternations of the stimuli (Logothetis, Leopold & Sheinberg, 1996; Note, however, that this only happens when stimuli fall within a limited range of temporal and spatial parameters; otherwise, perception alternates with the eyes; Lee & Blake, 1999).

It seems reasonable to assume that neural evidence would help to resolve the apparent contradictions noted above. However, this evidence has thrown up new contradictions, with conclusions seemingly dependent on the method used. Single-unit studies in monkeys have shown that the percentage of neurons whose activity correlates with perception during rivalry increases gradually from early to late visual cortex: 18% of the neurons examined in V1/V2 showed activity modulations that correlated with the monkeys' reports, as did 38% of the neurons in V4 (Leopold & Logothetis, 1996), 43% of the neurons in area MT (Logothetis & Schall, 1989), and 90% in area IT (Sheinberg & Logothetis, 1997). All but one of the neurons in areas V1/V2, V4 and MT, whose activity reflected rivalry, were binocular (in area IT all cells are binocular). These findings are interpreted as indicating that rivalry is very unlikely to be the result of monocular neurons in striate cortex being inhibited, as this would cause any representation of the suppressed image to be removed from subsequent regions – which isn't the case (Leopold & Logothetis, 1996). The results instead support the view that rivalry occurs between representations that are encoded in the activity of many neurons in different visual areas, attempting to establish a consensus (of relevance here, it is likely that such a consensus would have to be retained in working memory for the multiple areas involved to remain coordinated).

On the other hand, fMRI results from humans have tended to support a view of rivalry as competition occurring not between representations, but between the inputs from different eyes. Rivalry is fully resolved by the time the image reaches stimulus-specific regions of the ventral stream (Lumer et al 1998; Lumer & Rees, 1999; Tong, Nakayama, Vaughn, & Kanwisher, 1998). A face, for example, will activate the fusiform face area (Kanwisher et al, 1997) when it is

dominant, and the activity will be reduced when it is suppressed. These changes are of the same magnitude as in real stimulus alternations. This is analogous to the single-unit finding that the majority of cells in area IT reflect visual awareness (Sheinberg & Logothetis, 1997), but similar effects have been found earlier in the visual system: V1 activity has been found to be coupled with perceptual alternations during binocular rivalry, increasing when subjects reported seeing a higher-contrast grating, and decreasing when they saw a lower-contrast one (Polonsky, Blake, Braun, & Heeger, 2000; fMRI responses in V1 are known to increase monotonically with stimulus contrast – Heeger, Huk, Geisler, & Albrecht, 2000 – so the magnitude of the fMRI signal can serve as a 'tag' for the two gratings in V1). Moreover, and in contrast to single-unit findings, fluctuations in V1 activity were roughly equal to those in neighbouring visual areas (V2, V3, V3a, V4). In particular, there was none of the systematic increase in rivalry-related activity in later areas found in single-cell studies. The average amplitude of the fluctuations in V1 activity during rivalry was 56% of that evoked by physical stimulus alternations. It has been claimed that this difference between rivalry-induced and physical alternations is due to the responses of only a subset of V1 neurons (monocular neurons responding to input from a specific eye) being modulated by rivalry, whereas physical alternations affect all neurons.

Further research supporting this view (Tong & Engel, 2001) used fMRI to investigate binocular rivalry in the blind-spot representation of V1 (where all neurons are monocular, responding only to input from the ipsilateral eye). Activity in this region of V1 increased when the grating presented to the ipsilateral eye was perceived, and decreased when the contralateral eye became

dominant. This change was of the same magnitude in rivalry and in physical alternations, leading to the conclusion that binocular rivalry is resolved in monocular visual cortex – which is in contrast not only to the gradual process observed in single-cell studies, but also to the previous findings of rivalry being mediated by binocular neurons (as blind-spot neurons are, by definition, monocular). A recent study (Haynes, Deichmann, & Rees, 2005) has even demonstrated that fMRI activity recorded from the LGN showed eye-specific modulation during rivalry. Regions of the LGN that showed strong eye preference also independently showed strongly reduced activity during binocular rivalry, when the stimulus presented to their preferred eye was suppressed.

The discrepancy between single-unit and fMRI findings on binocular rivalry may be due to a number of factors. First, the fMRI results do not, in themselves, mean that rivalry is resolved within V1 or the LGN (Polonsky et al, 2000). The results could, for example, mean that neural events underlying rivalry originate in these early regions and are propagated to later areas, but also that those events are initiated at later stages and propagated via feedback to V1 and the LGN. Furthermore, the two processes are not mutually exclusive. The correlative nature and poor temporal resolution of fMRI mean that the causal relation between activations in various areas cannot be deduced from the imaging data on its own, as demonstrated by findings on attention: Single unit studies (e.g. Motter, 1993; Reynolds, Pasternak, & Desimone, 2000) have shown attentional modulation of activity in extrastriate visual areas, but not in V1; this is inconsistent with a number of fMRI studies that showed robust attentional modulations of V1 (Kastner, De Weerd, Desimone, & Ungerleider, 1998; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Kastner, Pinsk,

Desimone, & Ungerleider, 2000; Ress & Heeger, 2003) and even LGN (O'Connor, Fukui, Pinsk, & Kastner, 2002) activity that demonstrate early attentional selection in the visual pathway. The contradiction was resolved by studies combining EEG with fMRI (Martinez, Vento, Sereno, Frank, Buxton, et al, 1999; Noesselt, Hillyard, Woldorff, Schoenfeld, Hagner, et al, 2002): EEG showed that the effects of attention on V1 activity do not take place during the initial stimulus-related response (60-90 ms), but modulation that is consistent with activity changes detected by fMRI takes place in the time range of 150-250 ms. In other words, V1 is 'reactivated' 150-250 ms after exposure to a stimulus within the locus of spatial attention. Due to the slow emergence of the fMRI Blood-Oxygen-Level-Dependent (BOLD) signal, activity detected by fMRI seems to reflect both feedforward processes and later feedback influences from other areas. Feedback from other areas could therefore account for the activation seen in V1/LGN with fMRI but lacking in single-cell studies of rivalry.

This ties in to recent findings concerning the relationship between single-unit neural activity and the BOLD response. The fMRI signal is roughly proportional to local average firing rates (Heeger et al, 2000; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Rees, Friston, & Koch, 2000). But there is also evidence that the BOLD contrast mechanism reflects not only spiking output (as single-unit recordings do) but also input from different brain regions and subthreshold synaptic activity, such as that arising from simultaneous excitation and inhibition (Logothetis et al, 2001; Logothetis, 2003); Such activity would be invisible to an extracellular electrode, but may be of crucial importance in

rivalry; top-down feedback projected from neurons in other brain regions would therefore be picked up by fMRI but not necessarily by single-unit recordings.

Finally, the discrepancy may have resulted from the fact that single-unit studies (Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997) reported only the percentages of neurons whose activity was modulated by rivalry. The BOLD signal depends not only on the number of active neurons, but also on their firing rate. When single-unit data were reanalyzed (Polonsky et al, 2000), computing the average firing-rates during rivalry and physical alternations, the modulations in firing rate during rivalry (compared to physical alternation) were indeed similar in V1, V2 and V4 – though still only about half as large as those seen with fMRI. This new discrepancy can be explained by the fact that single-unit studies found different sub-populations of cells in areas MT, V4 and IT. Among these were cells whose responses correlated with reports during rivalry, and others whose responses anti-correlated with the reports; fMRI data averages indiscriminately across sub-populations, confounding the relative numbers of neurons in each category with their firing rates.

In conclusion, the differences between single-unit and fMRI findings are not as big as a first reading of the above results suggests. More importantly, the way the discrepancy may arise is directly related to the possible activity of top-down control mechanisms operating in a way that would be picked up by fMRI, but not by extracellular electrodes.

5.2.2 Binocular rivalry and mechanisms of top-down control

The above review indicates that it is probably an oversimplification to think that rivalry is fully associated with any single part of the visual system. A more refined view emerging from the literature is that rivalry is not a unitary phenomenon, resolved in a single neural locus (Blake & Logothetis, 2002; Tong, 2001). Rather, a number of separate stages are probably involved, in different locations along the visual pathways. To understand the interactions that lead to the emergence and characteristics of binocular rivalry, it may prove fruitful to focus on the factors that affect the temporal dynamics of rivalry.

Manipulating low-level physical properties (such as luminance, contrast, contour density and velocity) can affect suppression times. 'Stronger' images (e.g., ones with higher contrast) are suppressed for shorter periods. Interestingly, this does not affect dominance phases, whose length is generally not altered by such manipulations (Blake, 2001; Blake & Logothetis, 2002). In contrast, higher-level attributes affect dominance times. An image will dominate for longer periods when it is more meaningful; for example, upright faces dominate for longer periods than inverted ones (Blake, 2001). Also, images dominate for longer periods if they are surrounded by a context that fits them well (e.g., gratings that are co-aligned with a rival grating) than if their context does not (e.g., gratings that are orthogonal to a rival grating; Blake & Logothetis, 2002). Suppression times are usually not effected by these factors – context may maintain the dominance of a rival image, but will not encourage a suppressed image to escape from suppression (Sobel & Blake, 2002). The distinction between the effects of high- and low-level attributes on rivalry indicates that the

processes responsible for implementing and maintaining suppression may be distinguishable from those selecting an image for dominance (Sobel & Blake, 2002). The latter may involve high-level control regions previously implicated in working memory and attentional control.

Support for this hypothesis comes from recent fMRI studies (Lumer et al, 1998; Lumer & Rees, 1999), which identified a network of cortical regions whose activity covaried with perceptual switches during rivalry. The cortical regions involved included not only parts of the extrastriate cortex and the ventral visual pathway, but also fronto-parietal regions (**Figure 5.3**) previously shown to be involved in processes of attention (e.g., Wojciulik & Kanwisher, 1999) and working memory (e.g., Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; see also Naghavi & Nyberg, 2005). The studies included a binocular rivalry condition, as well as a control condition where physical alternations of monocular stimuli were presented ('replay'). Whereas extrastriate regions were also activated by nonrivalrous perceptual changes in the replay condition, activity in frontoparietal cortex was specifically associated with the dominance shifts experienced during rivalry. It is worth noting that an fMRI study examining perceptual shifts of nonrivalrous bistable images, such as the Rubin face-vase, also found activity related to transitions in a similar network (Kleinschmidt et al, 1998).

These results were interpreted as suggesting a major role for fronto-parietal areas in visual awareness. As these regions have previously been implicated in attention and working memory, their involvement in perceptual shifts may reflect the activity of a mechanism responsible for the selection of neuronal events for representation in awareness.

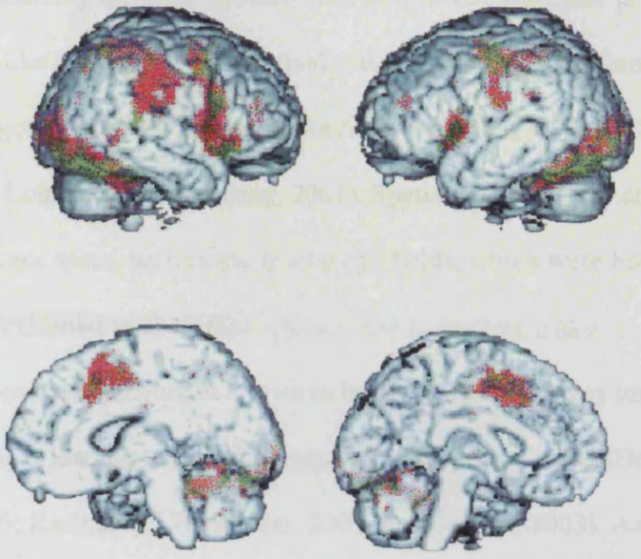

Figure 5.3. Brain activity associated with binocular rivalry transitions. Medial and lateral brain surfaces, upon which are superimposed areas where activity was specifically related to perceptual transitions in binocular rivalry (red) or in the replay condition (green). Note the widespread activity of a fronto-parietal network involved in rivalry transitions. From Lumer et al (1998).

However, the nature of this postulated mechanism requires further elucidation. The activity itself does not reveal whether the role of the fronto-parietal network might be to maintain current preferences, initiate shifts, or just monitor their occurrence. The possibility that activity in these regions is simply related to the generation of motor reports about perceptual shifts was ruled out in one of the studies mentioned above (Lumer & Rees, 1999), as that study only observed correlated activity between brain regions, without a task or perceptual report. However, the fronto-parietal activity could still be generated by a system registering perceptual changes, with no causal involvement in them. In addition, although the regions found to be involved in rivalry transitions are known to be

involved in directing attention spatially, this may not be their role in binocular rivalry, as unlike selective attention, rivalry is not amenable to voluntary control (Blake & Logothetis, 2002; Brown & Norcia, 1997; Meng & Tong, 2004; Sheinberg & Logothetis, 1997; Tong, 2001). Spatial attention also engages other visual and motor areas, such as the frontal eye fields, which were not activated during rivalry (Lumer et al 1998).

A fronto-parietal network is known to be involved in working memory and spatial attention, leading to biased perception in attentional tasks (Desimone & Duncan, 1995; Kastner & Ungerleider, 2001; Pessoa et al, 2003). As binocular rivalry engages this network in the absence of an explicit attentional effort, it follows that fronto-parietal regions may play a general role of maintaining perceptual biases between competing stimuli. The competition itself may occur anywhere along the visual stream. It is likely, though, that the activity of the fronto-parietal network reflects not the competition itself, but the biasing signal required to maintain perceptual preferences – just as is the case in selective attention (Kastner & Ungerleider, 2001; Pessoa et al, 2003).

Evidence supporting this notion comes from several sources. One is patient research: Various relevant abnormalities have been observed in patients with frontal or parietal lesions. These include a slowing-down of binocular rivalry compared to healthy controls (Pavlovskaya, Bonneh, Soroker, Sagi, & Ring, 2001). Alterations in other bistable phenomena have also been reported. Left hemisphere damage is associated with less disappearance during motion-induced blindness (Pavlovskaya et al, 2001), and patients with frontal and parietal lesions are significantly impaired in discovering the alternative interpretations of ambiguous figures (Ricci & Blundo, 1990; Meenan & Miller, 1994).

Another line of evidence is research on the involvement of memory mechanisms in rivalry. In a recent set of studies, Leopold's group demonstrated that if bistable images (among them binocular rivalry) are physically removed, and shown again after a while, there is a very good chance that the initial percept will be the same as it was before the removal (Leopold, Wilke, Maier, & Logothetis, 2002). Interestingly, this is the case even if other bistable images are presented in the intervening period (Maier, Wilke, Logothetis, & Leopold, 2003), indicating that a form of perceptual memory is probably involved. Recent unpublished data (P. Sterzer and G. Rees, personal communication January 2006) has shown that the magnitude of such perceptual memory effects is correlated with activity in regions of frontal cortex previously associated with working memory.

The above evidence provides strong support for the idea that a fronto-parietal network is responsible for the generation of top-down control signals that bias visual competition. However, neuroimaging only observes correlations between brain activation and behaviour; In order to ascertain that top-down control mechanisms indeed play a causal role in binocular rivalry, it would be necessary to manipulate such a system experimentally and observe the effect this has on perceptual alternations in rivalry. It has been previously shown that loading working memory impairs control of selective attention tasks (De Fockert et al, 2001; Lavie, 2000; Lavie & De Fockert, 2005; Lavie et al, 2004). The following sections of this chapter investigate whether this also occurs in binocular rivalry.

5.3 Experiment 11

5.3.1 Introduction

According to load theory (Lavie 2000; 2005; Lavie et al 2004), working memory is required whenever it is necessary to maintain priorities in order to deliberately ignore salient irrelevant stimuli. Here I propose that working memory may be required to actively maintain biases during competitive interactions in vision, not just when stimuli are deliberately ignored, but whenever visual competition requires the suppression of one stimulus in favour of another. This hypothesis was tested by manipulating working memory load during binocular rivalry.

If working memory is critical for active maintenance of perceptual biases during binocular rivalry, then high working memory load should alter the dynamics of this fundamental form (Blake, 2001; Blake & Logothetis, 2002) of visual competition, where one image is suppressed while another dominates awareness. Specifically, the ability to maintain a stable percept should be impaired, leading to a shortening of dominance phases (when a single monocular percept is experienced) and an increase in the duration of mixed-perception periods (when neither image is entirely suppressed, as typically occurs initially).

5.3.2 Method

Participants: Twelve naïve participants (8 female, mean age 26.08, range 17-32) gave informed consent to participate in the experiment. All participants had normal or corrected-to-normal vision.

Apparatus and stimuli: Participants sat in a dark sound-protected room, viewing a 20'' screen (Sony GDM-F520, resolution 640*480, 60 Hz refresh rate) from a distance of 100 cm, and wearing headphones. Stimuli were created and presented using Matlab on a Dell PWS650. Participants wore LCD shutter goggles (stereoeyes by StereoGraphics inc.) that alternated at 60 Hz in synchrony with alternate presentations of each of the two binocular rivalry stimuli, so each eye saw a different image every screen refresh cycle.

During binocular rivalry, each eye was presented with achromatic diagonal (±45° from vertical) orthogonal Gabor patches (a sinusoidally modulated carrier of wavelength 0.31°, drifting at 2 cycles/sec, convolved with a Gaussian envelope with sd 0.51°), displayed at 100% contrast with the same average luminance as the grey background (60 cd/m^2). Each participant viewed a single combination of Gabor orientation and drift direction, but all four combinations that comprise one leftward-drifting patch and one rightward-drifting patch were used across participants. Each Gabor was surrounded by nonius lines and a dartboard ring (diameter ~7.5°-14°) to promote stable binocular alignment. A small red fixation point was superimposed centrally.

Design: Perceptual alternations in binocular rivalry were measured while load in a working memory task was varied (**Figure 5.4**). On each trial, participants first memorized digits spoken in either a fixed ascending order (low load) or in random order (high load). Then, during a memory-retention interval, two orthogonally oriented Gabor patches were presented dichoptically, resulting in binocular rivalry. Participants reported their percepts continuously while viewing the rivalry stimuli. An auditory memory probe followed visual stimulus offset. To test the efficacy of the memory manipulation, accuracy rates and reaction times to the memory probe were recorded. To test the effect of the working memory manipulation on the temporal dynamics of binocular rivalry, two mathematically independent measures were obtained: The duration of the initial mixed period (the time from stimulus onset to the beginning of the first dominance phase, where one of the rivalling stimuli is entirely suppressed); and the duration of individual dominance phases.

Procedure: Each trial began with a blank grey screen. Participants were presented with the memory set through earphones: The word "ready" was followed by six digits, presented over six seconds. In the low load condition, the digits were always in the order 0, 1, 2, 3, 4, 5. In the high load condition 0 was followed by the digits 1-5 in random order, with the constraint that sets could not include three or more consecutive digits. After an additional 500 ms, the binocular rivalry stimuli appeared and were presented continuously for 10 s. Participants pressed one of two keys (the left and right arrows) to indicate which of the two Gabor patches was currently visible, releasing the keys during

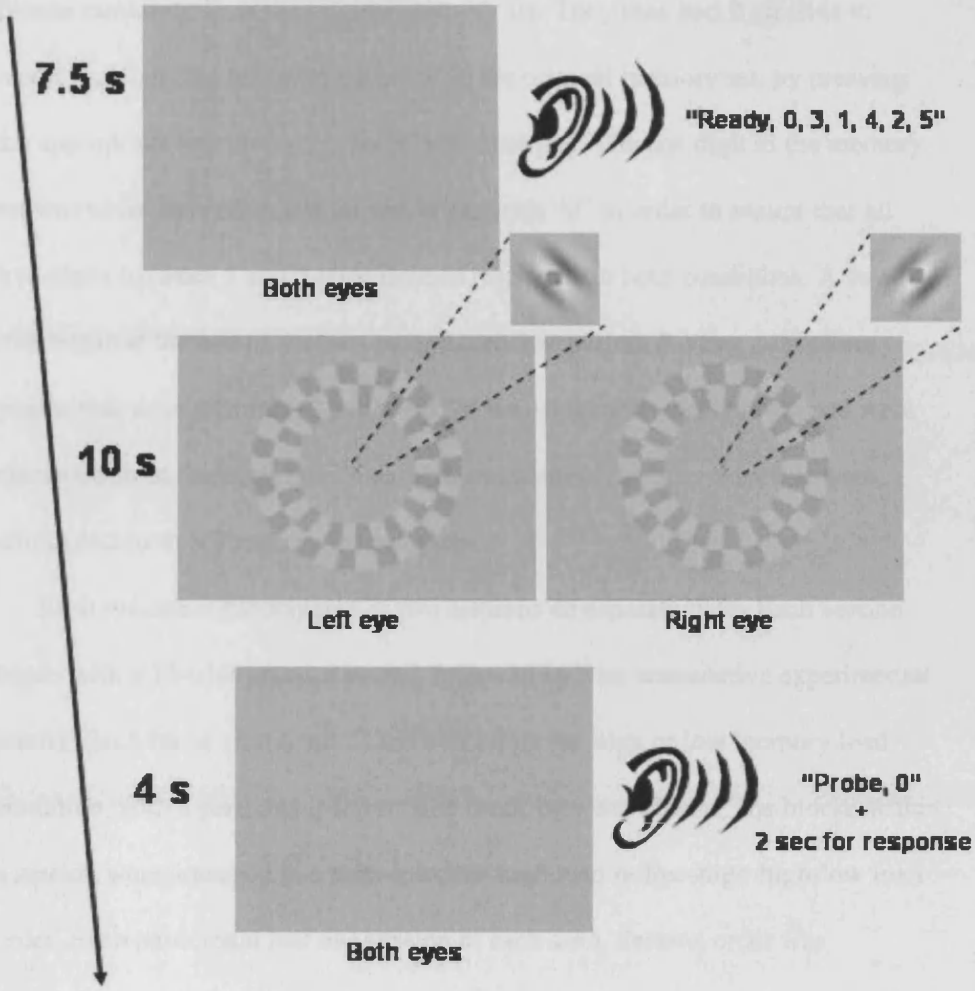

Figure 5.4. Experiment 11: Sequence of events in a high working memory load trial. Under low load, the memory set was always '012345'. Under high load, sets could not include three or more consecutive digits. At test, participants were instructed to report the digit that followed the probe in the original memory set (e.g., for the trial illustrated, the correct response is "3").

mixed periods where neither patch was entirely suppressed. At the end of the rivalry period the visual stimuli were replaced by a blank grey screen, and memory was tested: Participants heard the word "probe" followed by a digit

chosen randomly from the original memory set. They then had 2 seconds to report the digit that followed the probe in the original memory set, by pressing the appropriate key on the keyboard's number pad. The last digit in the memory set was never the probe, and all sets began with "0" in order to ensure that all five digits between 1 and 5 were used as responses in both conditions. A new trial began at the end of the two second response period. Rivalry dominance phases that were terminated by the end of the 10 second retention interval were discarded from the analysis. Trials with an incorrect memory response were eliminated from RT and rivalry analyses.

Each volunteer participated in two sessions on separate days. Each session began with a 16-trial practice period, followed by four consecutive experimental blocks. Each block contained 21 trials of either the high or low memory load condition, with a participant-terminated break between blocks. The blocks within a session were arranged in a high-low-low-high load or low-high-high-low load order. Each participant had one session of each kind. Session order was counterbalanced across participants.

5.3.3 Results and discussion

Working memory: RTs were significantly longer under high ($\underline{M}$ = 799 ms) than under low ($\underline{M}$ = 401 ms) working memory load ($t_{(11)} = 11.926$, $\underline{SEM}$ = 33.39, $p < 0.001$). In addition, accuracy rates were significantly lower under high ($\underline{M}$ = 89%) than under low ($\underline{M}$ = 99%) working memory load ($t_{(11)} = 6.075$, $\underline{SEM}$ = 0.016, $p < 0.001$).Taken together, these results confirm that the manipulation of memory load was effective.

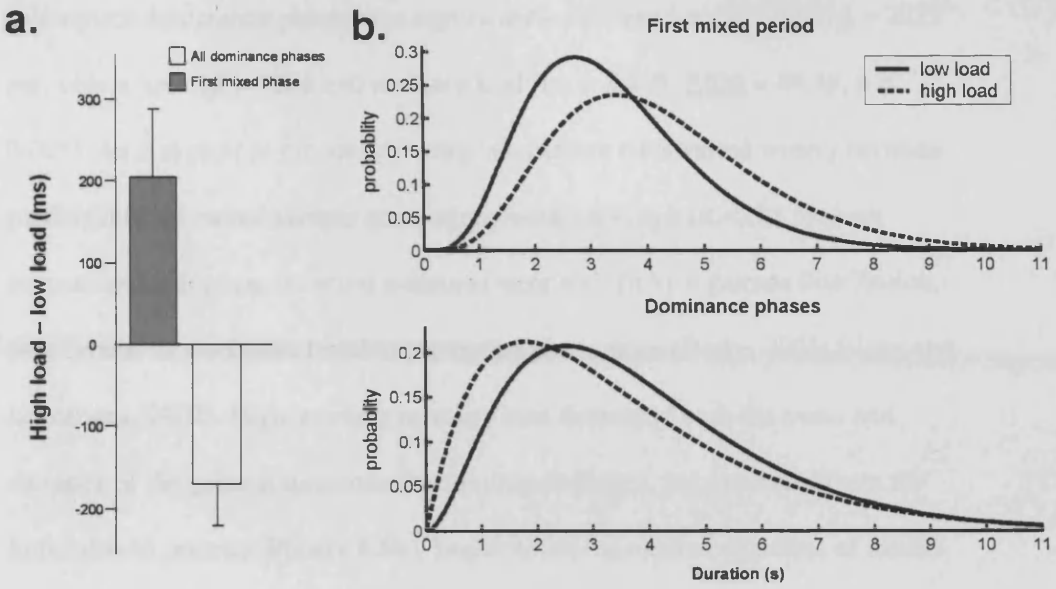

Figure 5.5. Experiment 11: High working memory load affects perceptual dynamics of binocular rivalry. (a) Mean differences for two dependent measures of rivalry under two different working memory load conditions, averaged over twelve participants. High (versus low) working memory load increased the median duration of the initial mixed period, and decreased the median duration of dominance phases. Error bars represent one SEM. (b) Best-fit gamma functions for the frequency distribution of initial mixed percept (top) and overall dominance phases (bottom) are plotted for one illustrative participant. Dominance durations are well fitted by a gamma function that has a smaller mean and variance under high (versus low) working memory load. The opposite pattern is apparent for initial mixed period durations.

Binocular rivalry: Critically, high working memory load had a significant effect on the two independent measures of perceptual dynamics in the binocular rivalry task (**Figure 5.5a**). First, the median[1] duration of the first mixed period increased with high ($\underline{M}$ = 1901 ms) versus low ($\underline{M}$ = 1696 ms) working memory load ($t_{(11)} = 2.434$, $\underline{SEM} = 84.27$, $p = 0.03$). Second, the median duration of

[1] Medians, rather than means, were used in the analysis due to the skewed nature of binocular rivalry durations (Blake, 2001). However, all results showed similar patterns for means as well.

subsequent dominance phases was significantly shortened under high (M = 2035 ms) versus low (M = 2206 ms) memory load ($t_{(11)} = 3.455$, SEM = 49.39, p = 0.005). As is typical in binocular rivalry, alternation rates varied widely between participants but paired sample correlations were very high (R=0.98 for both measures). Both phase duration measures were well fit by a gamma distribution, as is typical of stochastic bistable perceptual phenomena (Blake, 2001; Blake and Logothetis, 2002). High working memory load decreased both the mean and variance of the gamma functions for dominance phases, but increased them for initial mixed periods (**Figure 5.5b**). Importantly, the median durations of mixed-percept periods following the first one did not significantly differ comparing high (456 ms) and low (513 ms) load ($t_{(11)} = 0.996$, SEM = 57.17, *ns*). The opposite trend to that found for the initial mixed period indicates that the shortening of dominance phases cannot be attributed to an increase in the duration of mixed periods between the dominance phases.

The results are therefore consistent with the prediction that high working memory load would alter the dynamics of binocular rivalry, by impairing the visual system's ability to maintain a stable percept. Thus, under high memory load dominance phases were shortened and the duration of the initial mixed period increased. Due to technical limitations (the presence of the shutter goggles), it was not possible to monitor participants' eyes during the experiment, so the possibility of differences in eye movements or pupil diameter under different memory load conditions could not be ruled out. However, because of the technical difficulties involved in eye-tracking during binocular rivalry there is currently no available evidence on any systematic effects such eye-related factors may have on rivalry. It is therefore impossible to predict the possible effects of

such differences. A different problem, which could be addressed within the current dataset, is the possibility of sampling bias, which is explored next.

Analysis with a fixed sampling window: The initial mixed periods of binocular rivalry were longer under high working memory load (vs. low load). As the duration of binocular rivalry stimuli was fixed at 10 seconds under both load conditions, this meant that in each trial, there was less time left for dominance phases under high load than under low load. Potentially, this could have led to a systematic bias, where shorter dominance phases were more likely to be recorded under high load. This would account for the finding that dominance phases were shortened under high load. To rule out this possibility, a re-analysis of the experimental data was carried out, imposing a uniform sampling window (beginning at the end of the first mixed period of each trial) on both conditions, and using only trials that could fit the entire fixed window in. The duration of this window was chosen for each participant individually, to maximize the amount of data kept. On average, 74% (sd 10%) of the dominance phases in each condition were kept. Imposing the uniform-duration sampling window from the end of the first mixed period of each trial did not alter the effect of load on median dominance ($\underline{M}$ = 2161 ms and 1947 ms for low and high load, respectively; $t_{(11)} = 2.756$, $\underline{SEM} = 77.43$, $p = 0.019$).

To further rule out the possibility that the shortening of dominance phases under high load was an artifact of the longer initial mixed period, a computational simulation was carried out. This simulation is described in the next section.

5.4 Computational simulation

5.4.1 Introduction

Imposing a fixed sampling window on the binocular rivalry data of Experiment 11 showed that the shorter dominance phases under high working memory load are unlikely to have been due to the longer initial mixed period in this condition curtailing the sampling window for subsequent dominance phases. In order to further verify that the reduced sampling window under high working memory load could not account for the observed effect of load on dominance phase duration, a simple computational model was created. The model simulated the way changes in the sampling window would affect the average duration of dominance phases. The best-fit gamma distributions obtained for each participant's data were used to create simulated trials of two kinds: ones where the initial mixed period was sampled from the low load distribution and ones where it was sampled from the high load distribution. Importantly, the remainder of a simulated 10-second period was then filled with dominance-phase durations sampled from the *same* (low load) dominance phase distribution. Therefore, if the difference between dominance durations under high and low load is indeed an artefact, it should arise in the simulation as well.

5.4.2 Method

For each participant's data, the model took the best-fit gamma distribution parameters for the duration of the initial mixed phase under both high and low memory load, and the best-fit gamma distribution parameters for dominance phases under low load. Using these parameters, the model simulated 10 second 'trials' for high and low working memory load. The initial mixed period was sampled randomly from either the high or low load gamma distribution, and the remainder of the time was filled by sampling randomly from the participant's low load gamma distribution for dominance phases (using the same distribution for both working memory conditions). As in the rivalry experiment, dominance phases whose addition caused the duration of a simulated trial to exceed 10 seconds were discarded (See **Figure 5.6**). Simulated trials were iteratively generated until 2000 dominance phases were collected for each working memory condition. The median length of these dominance phases was then calculated. This procedure was repeated 1000 times for each participant's data, and the median dominance phases collected for each working memory condition were averaged. To verify that this simple model was indeed able to show effects of working memory load, the simulation was also run using the best-fit gamma distribution parameters for participants' dominance phases under high load (in simulated trials that were created with a high-load initial mixed percept).

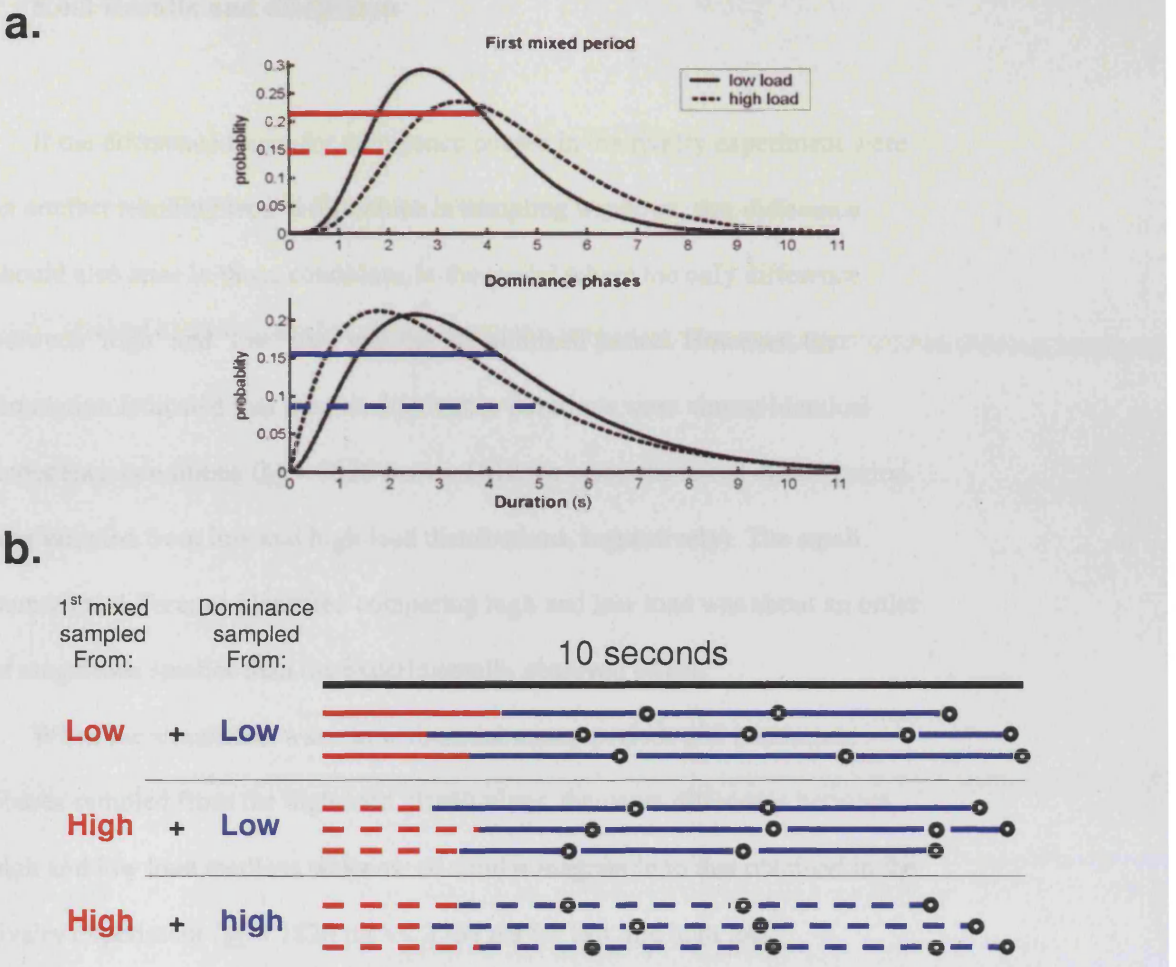

Figure 5.6. Sampling and trial structuring in the computational simulation. (a) Durations for first mixed periods and for dominance durations were sampled from the appropriate gamma distributions for each of the subjects who participated in Experiment 11. The red lines indicate sampled durations of first mixed periods, and the blue lines indicate sampled durations of dominance phases. Continuous lines are for durations sampled from the low load condition, and dashed lines indicate durations sampled from the high load condition. (b) Individual 10-second 'trials' were created by sampling an initial mixed period from the appropriate first-mixed-period gamma distribution, and then filling the remainder of the 10-second period with dominance phases sampled from the appropriate dominance-phase gamma distribution.

5.4.3 Results and discussion

If the difference found for dominance phases in the rivalry experiment were an artefact resulting from a difference in sampling windows, this difference should also arise in those conditions in the model where the only difference between 'high' and 'low' load was the initial mixed period. However, the simulation indicated that median dominance durations were almost identical under such conditions ($\underline{M}$ = 1826 ms vs. 1812 ms when the initial mixed period was sampled from low and high load distributions, respectively). The small numerical difference identified comparing high and low load was about an order of magnitude smaller than the experimentally observed effect.

When the simulation was run with initial mixed periods and dominance phases sampled from the high-load distributions, the mean difference between high and low load medians was now of similar magnitude to that obtained in the rivalry experiment ($\underline{M}$ = 1826 ms vs. 1704 ms for low and high load, respectively, a difference of 122 ms compared with 171 ms in Experiment 11).

Thus, a difference between high and low working memory load in the duration of the initial mixed percept cannot account for the difference found in the duration of subsequent dominance phases. A sampling bias, therefore, cannot account for the results of Experiment 11.

These results can also not be accounted for by high load leading to a more stringent criterion for reporting dominance. If this were the case, all mixed periods, not just the first, should have been longer under high memory load. Instead, these findings suggest that once the visual system began experiencing rivalry, the full sequence of perceptual transitions became quicker under high

load. Nevertheless, it remains unclear whether high working memory load specifically reduces the ability to actively maintain perceptual choices in cases of visual competition (such as binocular rivalry), or whether it simply alters the characteristics of responses to visual events. This issue was addressed in Experiment 12.

5.5 Experiment 12

5.5.1 Introduction

Experiment 11 showed that under high working memory load, participants reported shorter dominance phases and longer initial mixed periods than under low working memory load. These results are consistent with the hypothesis that working memory is involved in maintaining perceptual biases in binocular rivalry. However, it remains possible that the above results may be due to a change in response characteristics under high (vs. low) working memory load, rather than a true perceptual alteration.

If the results of Experiment 11 were indeed due to high working memory load altering the characteristics of responses to visual events, then loading working memory should also have an effect on responses to gradual *physical* changes in a stimulus. Another experiment was therefore conducted, where participants responded to gradual physical transitions between orthogonally oriented Gabor patches presented in similar fashion to the rivalry experiment, except the same image was now presented to both eyes. These transitions did not

involve competition, but otherwise kept the characteristics of binocular rivalry and produced a similar perceptual experience.

If high working memory load causes a change in response characteristics that brings about reports of shorter dominance phases in binocular rivalry, this should lead to a predictable pattern of results for physical transitions. Reported 'dominance' phases (i.e. the presence of a single image) should be shorter under high working memory load. This would be due to either or both of two measures. Responses to the onset of gradual changes could occur earlier, and/or the reported durations of such transitions could be longer under high than under low working memory load. The effect of working memory load on the initial mixed period of binocular rivalry could, potentially, be due to a longer time taken to generate a response under high load, rather than a longer period required for the visual system to establish a dominant percept. If this were the case, then this difference should arise even when only a single image (rather than rivalrous ones) is presented at trial onset.

5.5.2 Method

Participants: Six new volunteers (2 female, mean age 27.83, range 22-32) participated in the experiment. All participants had normal or corrected-to-normal vision.

Apparatus and stimuli: Set-up was very similar to that of Experiment 11, except for a few important differences. The LCD shutter goggles worn by the participants were constantly transparent during the ten-second memory retention

period; stimuli were presented binocularly and did not undergo rivalry. Each retention interval began with the presentation of a single Gabor patch, so there was no initial mixed period. The Gabor patch underwent a gradual physical transition, intermittently and randomly (1-3 occurrences per trial, at random times), being replaced by an orthogonally oriented Gabor. Physical stimulation parameters were kept identical to those of Experiment 11 by alternating the Gabor patches at 60 Hz. Gradual transitions were produced by decreasing the contrast of the original stimulus progressively (from 100% to 0) while the contrast of the newly visible orthogonal stimulus was increased (from 0 to 100%) over a period of 3150 ms. Such a gradual transition subjectively approximated the appearance and duration of the rivalrous transitions reported in Experiment 11, giving rise to a very similar (but binocularly presented and non-rivalrous) mixed percept.

Design: The design was identical to that of Experiment 11, the only difference being that instead of the binocular rivalry stimulus, here the same Gabor patches underwent gradual physical alternations. As in Experiment 11, accuracy rates and reaction times to the memory probe were recorded to test the efficacy of the memory manipulation. Three dependent measures were recorded to test the effect of the working memory manipulation on patterns of response to non-rivalrous visual transitions: The reaction time to the onset of a physical transition between Gabor patches; the reported duration of mixed phases; and the time from trial onset (the presentation of the first Gabor patch at the beginning of the 10-second visual stimulation period) to the first perceptual report.

Procedure: The procedure was identical to that of experiment 11, except that during each trial participants reported physical changes in the stimuli rather than phenomenal ones. As in Experiment 11, participants reported their percepts using two keys (the left and right arrows) to indicate exclusive perception of either orthogonal grating, with both keys raised indicating mixed perception. As there was no initial mixed period in this experiment (after presentation of the memory set, a single Gabor patch appeared), participants were instructed to press the appropriate key as quickly as possible after the onset of visual stimuli. Perceptual report data were only analyzed from correct working memory trials.

5.5.3 Results and discussion

Working memory: The manipulation of working memory load was again effective, and comparable to that in Experiment 11. Mean RTs to the memory probe were longer and accuracy lower under high working memory load (M = 962 ms, 83% accuracy) than under low load (M = 471 ms, 99% accuracy; $t_{(5)}$=15.734, p = 0.001 for the RTs, $t_{(5)}$=4.637, p = 0.006 for the accuracy).

Binocular physical transition responses: Mean RTs to the onset of physical transitions were significantly longer under high versus low working memory load (1698 ms vs. 1643 ms, respectively; $t_{(5)}$=3.440, SEM = 15.99, p=0.018). Note that this effect is in the opposite direction to that predicted if the results of Experiment 11 were due to changes in response characteristics under high working memory load. There was no significant effect of high versus low load on reports of mean duration of the mixed stimulus (800 ms vs. 824 ms, respectively;

$t_{(5)}$=0.625, SEM = 38.69, *ns*). Though not significant, the trend in the mixed-period duration reports is also in the opposite direction to that predicted if the results of Experiment 11 were due to changes in response characteristics under high working memory load. Working memory load, therefore, clearly does not simply speed up responses to visual events. Though such load does seem to have some effect on response characteristics, this effect is in the opposite direction to that found for binocular rivalry – implying that the actual perceptual effect in rivalry may have in fact been larger than participants' reports indicated.

The time taken to make the first response to the unambiguous stimuli at the beginning of each trial was longer under high than under low working memory load (622 ms vs. 554 ms, respectively; $t_{(5)}$=3.560, SEM = 19.15, p=0.016), but this effect is much smaller than observed for initial mixed percepts in binocular rivalry (68 ms here vs. 205 ms in Experiment 11), suggesting the effect in rivalry reflects a real perceptual effect, rather than just a slowing of the first response under high working memory load.

5.6 Chapter Discussion

The results described in this chapter demonstrate that as anticipated by the load theory (Lavie, 2000; 2005; Lavie et al, 2004), working memory load plays a role in determining the competitive dynamics in binocular rivalry. The results also highlight the specificity of working memory load effects to rivalry (as opposed to the non-competitive physical transitions in Experiment 12). Loading working memory rendered it unavailable to exert top-down control maintaining the dominant percept in binocular rivalry. Thus the duration of the initial mixed

percept was increased, the suppressed image escaped suppression more easily, and subsequent dominance phases were truncated. Working memory can therefore play a role in visual competition even in the absence of explicit instruction to ignore a distractor: These results imply that working memory may be essential in biasing visual competition whenever such competition arises, and not just in selective attention tasks as shown previously (De Fockert et al, 2001; Lavie, 2000; Lavie & De Fockert, 2005; Lavie et al, 2004).

These results also shed light on the mechanisms involved in binocular rivalry, favouring a view of it as a complex, multilevel phenomenon, rather than a purely low-level one: Even if the competition occurs in early stages of the visual stream (Polonsky et al, 2000; Tong & Engel, 2001), it can be systematically modulated by top-down signals. Unlike previous claims (Meng & Tong, 2004) binocular rivalry appears to be influenced by at least some level of top-down control.

The finding that working memory load leads to shorter dominance periods is in line with demonstrations that short-term memory plays a role in determining the percept in bistable images (including binocular rivalry). When such images are physically removed and then shown again after a while, the percept they evoke when shown again will typically be the same as it was before the removal (Leopold et al, 2002). Both findings indicate a role for memory in maintenance of the dominant percept. It is thus possible that the underlying mechanisms for the role of working memory in binocular rivalry overlap in the present study and these previous studies.

Though selective attention cannot prolong dominance phases indefinitely (Meng & Tong, 2004) or initiate perceptual transitions, it is still possible that it played a role in the present findings. Attention can modulate dominance

durations to a certain extent (Ooi & He, 1999); therefore, it is possible that the effect of working memory is brought about by participants paying less attention to the currently dominant stimulus under high working memory load, leading to a reduction in dominance durations.

Finally, these findings have important theoretical implications, as they suggest a general role for working memory in visual awareness. Memorizing auditory digits has very little in common with visual perception, yet strong interference between auditory working memory load and visual perception was observed. This is consistent with a general role for working memory in visual awareness – that of maintaining perceptual biases while constant incoming information works to destabilize them. We cannot be aware of all the visual information entering our eyes, so may depend on working memory to maintain our perceptual choices, enabling us to become aware of certain stimuli while rejecting others.

Chapter 6:

The role of right parietal cortex

in binocular rivalry

6.1 Chapter Introduction

The involvement of high-level brain regions and the top-down processes they mediate in the control of binocular rivalry has been widely debated (Blake & Logothetis, 2002; Tong, 2001). As reviewed earlier (**Section 5.2.2**), low-level physical properties of rivalling stimuli, such as contrast or luminance, influence suppression but not dominance durations. The opposite pattern is apparent for high-level features such as context or meaning (Blake, 2001; Blake & Logothetis, 2002; Tong, 2001). This distinction implies that the processes implementing suppression may be distinguishable from those maintaining the dominance of an image (Sobel & Blake, 2002). The association of dominance durations with the high-level attributes of images indicates that such selection and maintenance may involve top-down processes mediated by brain regions outside occipital cortex.

The involvement of top-down cognitive processes in the maintenance of perceptual biases in binocular rivalry was confirmed in the previous chapter, by showing that loading working memory reduces the visual system's ability to maintain a stable, biased percept in rivalry. However, to independently establish the role of high-level brain regions (as opposed to cognitive processes) in the control of rivalry, it is necessary to manipulate such regions directly. Previous fMRI studies (Lumer et al, 1998; Lumer & Rees, 1999) have demonstrated that a network comprising right-lateralized frontal and parietal areas is active during perceptual transitions in binocular rivalry. Though this implies that these regions may play a causal role in the control of rivalry, such a conclusion is precluded by the correlational nature of fMRI. As the low temporal resolution of fMRI makes

it impossible to determine whether the activation preceded or followed perceptual transitions, the activation found could, for example, be merely the result of a transition being noticed and then drawing attention (although this is somewhat unlikely, since physical transitions did not lead to similar activation despite the use of a replay procedure that made them hard to distinguish from rivalry transitions).

Even if a causal role for right-parietal activity were to be inferred, the neuroimaging data do not afford a straightforward interpretation of the nature of this role. On the one hand, the fact that right fronto-parietal activity was time-locked to transitions (Lumer et al, 1998) suggests that a signal originating in these regions may initiate the transitions. Alternatively, such activity may be related to a surge of metabolic demands in inhibitory synapses (Heeger & Ress, 2002; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Mathiesen, Caesar, Akgoren, & Lauritzen, 1998), as the maintenance of a stable bias is terminated. A further (though not exclusive) possibility is that such activity may reflect an increase in the metabolic demands of a subset of neurons attempting to maintain the current perceptual state, just prior to a different subset (promoting dominance of the other image) taking over. Finally, it is possible that the relative crudeness of the standard univariate fMRI analysis may not reveal the whole story: Recent research employing more sensitive multivariate analysis techniques has revealed activity in parietal regions associated with particular perceptual states in an ambiguous rotating sphere, a different kind of bistable stimulus (Brouwer, van Ee, & Tong, 2006); whether this will also be found for rivalry remains to be seen. The association of right fronto-parietal activity with binocular rivalry transitions does not, therefore, lend itself to a straightforward

interpretation. To clarify the role of these regions in rivalry it is necessary to employ a manipulative (rather than correlational) method such as Transcranial Magnetic Stimulation (TMS).

Previous studies using TMS to investigate binocular rivalry have not applied it to the right parietal region associated with perceptual transitions in fMRI. One study (Pearson, Tadin & Blake, 2006) applied single-pulse TMS at fixed time-intervals to occipital cortex while participants viewed a rivalrous stimulus, finding that the probability of a perceptual transition increased within the first post-stimulation second. This result suggests, unsurprisingly, that early visual cortex is critically involved in the processes underlying rivalry. However, it does not clarify what normal function is interrupted by the stimulation used. Such stimulation could, on the one hand, exacerbate local competitive interactions between neuronal subsets representing the competing stimuli, leading to faster resolution of the competition in favour of the suppressed stimulus; or it could, on the other hand, interrupt an external signal maintaining the current perceptual bias.

A different study (Miller et al, 2000) applied single-pulse TMS over left temporo-parietal cortex, time-locked to the onset of reported perceptual transitions in binocular rivalry. This led to a reversal of the transition (back to the pre-TMS percept; i.e. a very short dominance phase of the other image) for images presented to one of the two eyes, but not to the other. Again, this finding is difficult to interpret. First, time-locking the TMS pulses to reports of transition onsets means it is impossible to tell whether the reversals of the transitions were due to the interruption of a signal initiating the perceptual switch, or of a signal maintaining the new perceptual state. Furthermore, the left temporo-parietal

TMS stimulation site was approximate and not based on co-registration with any specific brain region; this limits any conclusions regarding the functional neuroanatomy underlying the effect.

6.2 Experiment 13

The purpose of the present study was therefore to examine whether the superior right parietal cortex, which has been previously (Lumer et al, 1998; Lumer & Rees, 1999) associated with activity during rivalrous perceptual transitions (and carefully localized here by co-registering individual participants' structural MRI scans to their heads), plays a causal role in the control of binocular rivalry. The parietal stimulation site was chosen rather than a frontal one as frontal TMS stimulation tends to cause discomfort to participants by stimulating the facial nerve. Working memory processes, such as those whose influence on rivalry was investigated in Chapter 5, are usually associated with frontal cortex activity. However, previous research actually shows that both working memory (Courtney et al, 1998) and visual short-term memory (Todd & Marois, 2004; Vogel & Machizawa, 2004) tasks are associated with activity in a network comprising both frontal *and* parietal regions, including the superior parietal region selected for TMS stimulation here. To avoid the uncertainties inherent in the use of online single-pulse TMS (see comments above on Miller et al, 2000; and Pearson et.al, 2006), this study employed repetitive TMS (rTMS), applied offline at 1 Hz for 30 minutes just prior to viewing the binocular rivalry stimulus. Such stimulation is believed to temporarily impair the normal activity

of the cortex region below the stimulation site (Walsh & Pascual-Leone, 2003). To control for non-specific effects of TMS, the homologous location in the left hemisphere (which has not been associated with binocular rivalry transitions; Lumer et al, 1998) was stimulated in a separate session. Temporarily impairing the activity of superior right parietal cortex should shed light on the role it plays in binocular rivalry: If the role of such activity is to initiate perceptual transitions, then impairing it should interfere with the initiation of transitions and lead to longer dominance durations; Conversely, if right parietal activity is necessary for maintaining a bias during visual competition, the impairment will interfere with this maintenance and lead to shorter dominance durations. Finally, if right parietal lobe plays no causal role in binocular rivalry, TMS stimulation should have no effect on dominance durations.

6.3 Method

Participants: 8 healthy volunteers gave informed consent to participate in the experiment. All volunteers had normal or corrected-to-normal vision. Two participants whose median dominance durations were over 2.5 standard deviations from the group mean (leading to a small sample of dominance durations) were regarded as outliers and their data were excluded from analysis. The remaining six participants had an average age of 30.2 (range 22-42). Three of them were female and all were right-handed.

Visual stimuli and apparatus: Participants sat in a dark room, viewing an 18'' screen (Dell UltraScan P991, resolution 640*480, 60 Hz refresh rate) from a distance of 60 cm. Stimuli were created and presented using Matlab on a Sony Vaio PCV-RS144 computer. Participants wore LCD shutter goggles (stereoeyes by StereoGraphics inc) which alternated at 60 Hz in synchrony with alternate presentations of each of the two binocular rivalry stimuli, so each eye saw a different image every screen refresh cycle.

During binocular rivalry, each eye was presented with achromatic diagonal (±45° from vertical) orthogonal Gabor patches (a sinusoidally modulated carrier of wavelength 0.31°, drifting at 2 cycles/sec, convolved with a Gaussian envelope with sd 0.51°), displayed at 100% contrast with the same average luminance as the grey background (60 cd/m^2). Each participant viewed a single combination of Gabor orientation and drift direction, but all four combinations that comprise one leftward-drifting patch and one rightward-drifting patch were used across participants. Each Gabor was surrounded by blue nonius lines and a dartboard ring (diameter ~7.5°-14°) to promote stable binocular alignment; a small blue fixation point was superimposed centrally (**Figure 6.1**).

TMS stimulation site localization: Each participant underwent an MRI session to obtain a structural scan. Structural MRIs were spatially normalized to a standard template based on the MNI reference brain (Talairach and Tournoux, 1988), using Statistical Parametric Mapping software (SPM2, Wellcome Department of Imaging Neuroscience, UCL). The site in the superior right parietal lobe previously associated with perceptual switches in binocular rivalry (x=36, y=-45, z=51, Lumer et al, 1998, **Figure 6.2**) and its homologue in the left

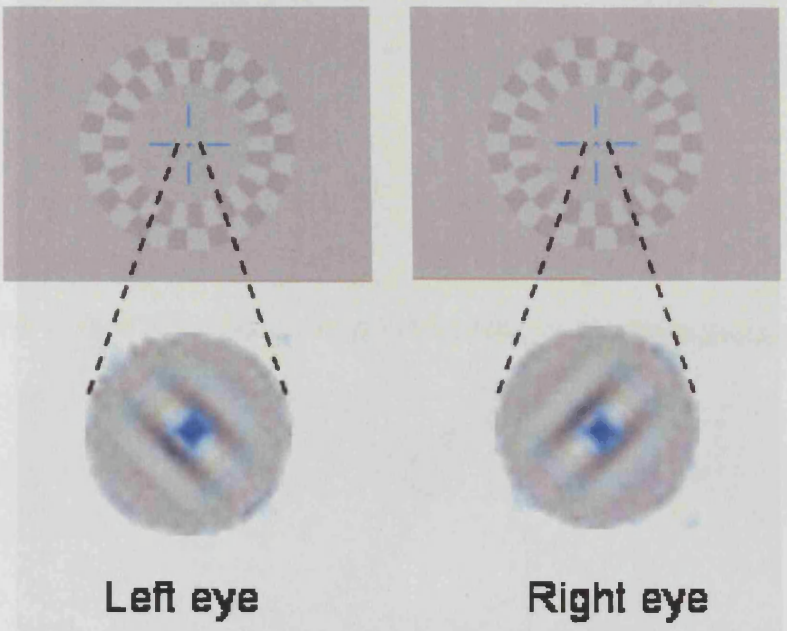

Figure 6.1. Experiment 13: The binocular rivalry stimulus. Each eye was presented with a drifting Gabor patch (shown here enlarged from the centre of the screen). The Gabors were oriented obliquely and orthogonally to each other. Fixation dots, nonius lines and dartboard rings helped maintain stable binocular alignment.

hemisphere (x =-36) were located and marked. The structural scans were then warped back to their original shape, and Brainsight software (Rogue Research, Montreal, Canada) was used to coregister each participant's structural scan to their head and to identify the scalp loci closest to the stimulation sites.

TMS stimulation parameters: In each TMS session (see procedure below), a Magstim SuperRapid TMS machine and a double 70 mm figure of eight coil were used to deliver repetitive TMS (rTMS) pulses at 1 HZ for 30 minutes. The coil was held against the participant's head by the experimenter, at an angle which would induce a current in a ventral-frontal direction (with the handle held

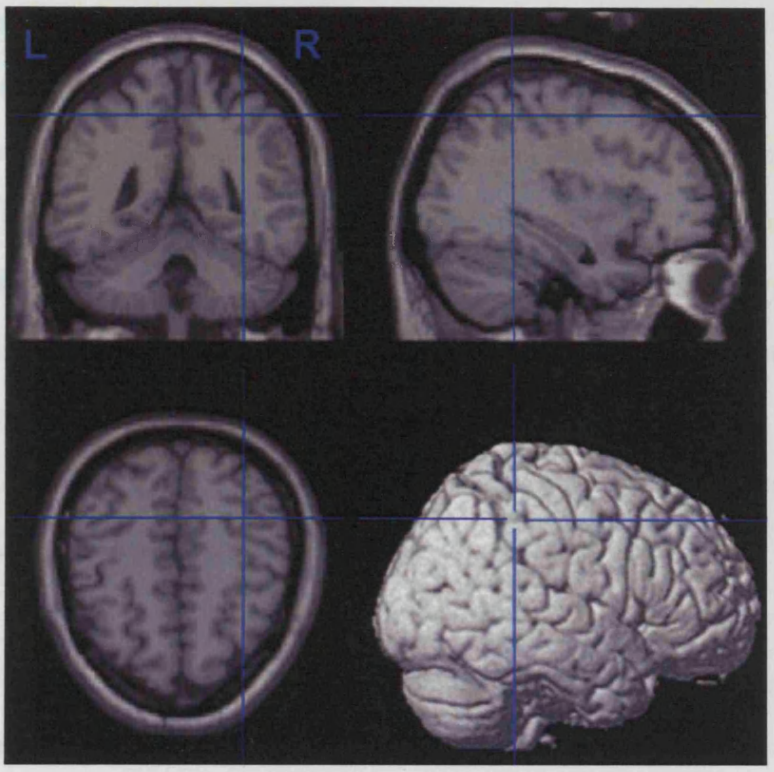

Figure 6.2. Experiment 13: TMS stimulation site in right parietal cortex. Crosshairs in the coronal, sagittal and horizontal views of a single participant's brain, and in a rendered SPM2 3D brain, show the location of MNI coordinates x=36, y=-45, z=51. The homologous site (x=-36) was stimulated in the left hemisphere. L: Left; R: Right.

up at an angle roughly 30° posterior from vertical). Stimulation intensity was determined individually for each participant before the experiment: The resting motor threshold was measured by stimulating left motor cortex and finding the minimum intensity which induced visible movement in the participant's index finger on half of 8-10 trials. TMS stimulation intensity was then set to 90% of the motor threshold, rounded to the nearest whole number (mean motor threshold: 51.7% of stimulator output, range 43-67%; mean stimulation intensity: 46.5% of stimulator output, range 39-60%).

Design and procedure: To investigate the role of right superior parietal cortex in binocular rivalry, participants viewed a binocular rivalry display and reported their percepts under three conditions: (1) No TMS, (2) Following right parietal stimulation, and (3) Following left parietal stimulation. Right parietal stimulation was delivered to the location previously associated with perceptual transitions in rivalry (Lumer et al, 1998), and the homologous location in the left hemisphere was used as a control site. Due to the skewed distribution of dominance durations in binocular rivalry, the median dominance durations for each eye under each condition were taken as dependent measures.

To avoid any carry-over effects of TMS stimulation, the experiment was carried out over three consecutive days, with each condition run on a different day. Order of conditions was counterbalanced across participants. At the beginning of the first TMS session, the participant's resting motor threshold was assessed (see TMS stimulation parameters above for assessment procedure), and TMS stimulation intensity was determined. Following this, and at the beginning of the second TMS session, the stimulation site for that session was located on the participant's scalp. 1 Hz TMS was then administered for 30 minutes. Immediately upon completion of the TMS stimulation (or at the beginning of the session in the no TMS condition) participants viewed the binocular rivalry display for four 2.5 minute blocks, separated by 20-second rest intervals. Participants reported their percepts continuously, using the left (left eye dominant), right (right eye) and down (mixed percept) arrow keys on a computer keyboard. Each key was held down for as long as its corresponding percept was visible.

6.4 Results

Median binocular rivalry dominance durations (**Table 6.1**) were entered into a two-way repeated-measures ANOVA, in which the factors were condition (3 levels: No TMS, right parietal TMS, left parietal TMS) and eye (2 levels: Right eye, left eye). The ANOVA revealed a significant main effect of condition ($F_{(2,10)}$ = 4.891, MSE = 457218.33 , p = 0.033). There was no main effect of eye ($F_{(1,5)}$ = 1.4, MSE = 110696.38, *ns*) and no interaction between condition and eye (F<1, *ns*). Dominance durations were therefore collapsed across eyes for follow-up comparisons. Paired-sample t-tests were used to compare no TMS versus right TMS and no TMS versus left TMS (**Figure 6.3a**). Right TMS was found to significantly shorten dominance durations compared with no TMS ($t_{(5)}$=2.761, SEM = 193, p=0.04), and compared with left TMS (though this comparison only reached significance at a one-tailed level; $t_{(5)}$=2.317, SEM = 336, p=0.034, one-tailed). There was no significant difference between left TMS and the no TMS condition ($t_{(5)}$=1.041, SEM = 237, *ns*). Note that the trend for longer (rather

Table 6.1. Experiment 13: Means of median dominance durations. Durations are given in ms. Numbers in parentheses indicate 1 standard error of the mean.

	No TMS	Right TMS	Left TMS
Right eye	3263 (330)	2657 (245)	3434 (348)
Left eye	3620 (634)	3037 (203)	3939 (624)
Both eyes	3365 (333)	2832 (166)	3611 (454)

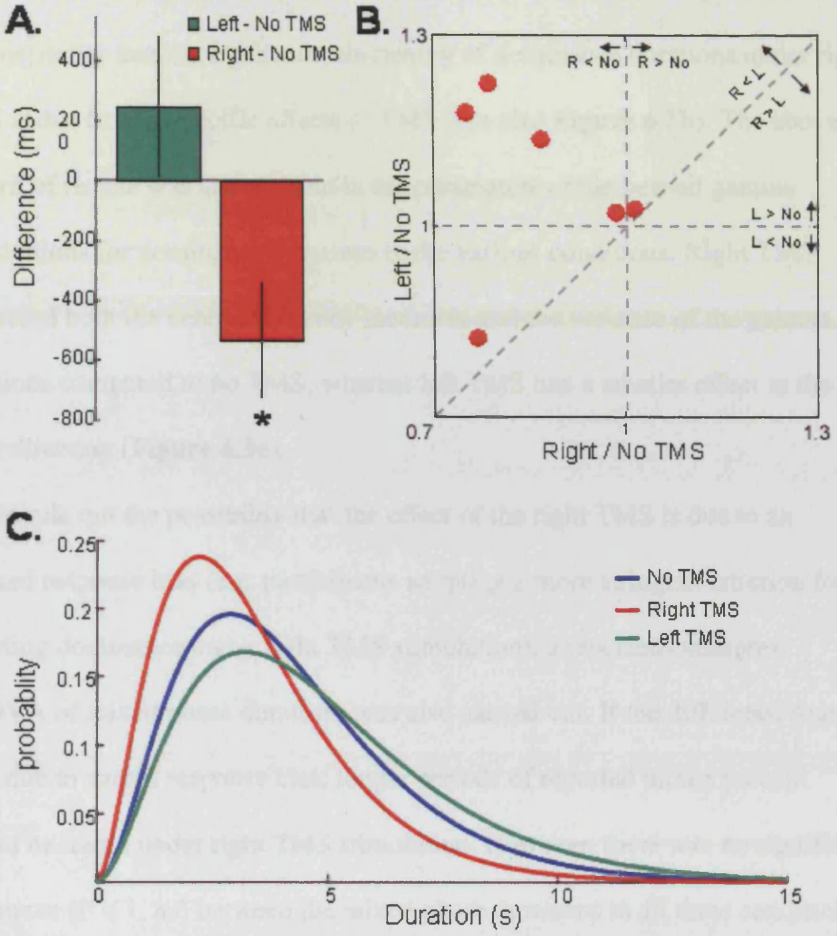

Figure 6.3. Experiment 13: Results. A. Mean differences of dominance duration medians for left and right TMS versus no TMS. Positive values indicate longer durations than under no TMS, and negative values indicate a shortening of dominance durations compared with no TMS. Error bars represent 1 standard error of the mean. * $p < 0.05$. **B.** Median dominance durations of individual participants in each TMS condition plotted as a fraction of their no-TMS median. Ratios greater than 1 indicate lengthening (compared to no TMS), and ratios smaller than 1 indicate shortening of dominance durations. Five of six participants fall to the left of the vertical dashed line, indicating a shortening of dominance durations under right TMS. All six fall to the left of the diagonal dashed line, indicating a shortening under right TMS compared to left TMS. Note that except for a single outlier (bottom left corner), there seems to be an inverse correlation between the effects of left and right TMS. R: Right TMS; L: Left TMS; No: No TMS. **C.** Best-fit gamma functions for the frequency distribution of dominance durations, plotted for one illustrative participant. Under right TMS, the gamma function (red) has a smaller mean and variance than under no (blue) or left (green) TMS.

than shorter) dominance durations under left TMS than under no TMS rules out the possibility that the significant shortening of dominance durations under right TMS is due to non-specific effects of TMS (see also **Figure 6.3b**). The above pattern of results was also evident in the parameters of the best-fit gamma distributions for dominance durations in the various conditions: Right TMS decreased both the central tendency measures and the variance of the gamma functions compared to no TMS, whereas left TMS had a smaller effect in the other direction (**Figure 6.3c**).

To rule out the possibility that the effect of the right TMS is due to an induced response bias (e.g. participants adopting a more stringent criterion for reporting dominance under right TMS stimulation), a repeated-measures ANOVA of mixed phase durations was also carried out. If the difference found were due to such a response bias, longer periods of reported mixed percept should be found under right TMS stimulation. However, there was no significant difference ($F < 1$, *ns*) between the mixed phase durations in all three conditions (average of medians: 1776, 1997 and 1647 ms for No TMS, right TMS and left TMS, respectively). The effect of right parietal TMS is also unlikely to be due to eye movement artefacts. Though the use of shutter goggles to create binocular rivalry precluded measurement of eye-movements, previous research has shown that such movements are not induced by TMS over posterior parietal cortex (Ashbridge, Walsh & Cowey, 1997; Wessel, Koempf, Klostermann & Moser, 1991; for a review, see Walsh and Pascual-Leone, 2003). Furthermore, there is no reason to assume differential, asymmetrical effects of TMS over right and left parietal cortices with respect to eye movements – yet an asymmetrical effect on binocular rivalry was found.

6.5 Discussion

Previous fMRI findings have shown that perceptual transitions in binocular rivalry are associated with transient activation in right superior parietal cortex (Lumer et al, 1998). However, the correlational nature of fMRI has made it difficult to assert that this region plays a causal role in such transitions (it may, for example, simply respond to their occurrence). Even if a causal role were assumed, the precise nature of this role could not be inferred from neuroimaging data alone. The purpose of the present study was therefore to directly perturb the activity of the relevant region in order to make such inferences.

1Hz rTMS stimulation of the superior right parietal lobe led to a significant shortening of dominance durations in binocular rivalry, compared with no TMS stimulation. In contrast, stimulating the homologous site in the left hemisphere led to a non-significant trend in the opposite direction. These results have important implications for our understanding of the involvement of high-level brain regions in the control of binocular rivalry.

The present results confirm that right superior parietal cortex (unlike left parietal cortex, which was not significantly activated in fMRI either; Lumer et al, 1998) does indeed play a causal role in the control of binocular rivalry, as disrupting its activity altered the temporal dynamics of rivalry. However, the results place critical constraints on our understanding of this role. Causing a temporary deficit in right parietal activity would have led to longer dominance durations if the role of such activity were to initiate perceptual transitions; it would lead to shorter dominance durations if right parietal activity was necessary

for maintaining a bias during visual competition. The present results clearly favour the latter possibility.

The use of offline rTMS in this study avoided the interpretation difficulties that are inherent to the use of online, single-pulse TMS in investigating binocular rivalry (Miller et al, 2000; Pearson et al, 2006). The effects of online TMS on binocular rivalry are ambiguous as they may be attributed to either interference with the initiation of a perceptual transition on the one hand, or to the perturbation of a maintenance signal on the other. Creating a temporary (but relatively prolonged) deficit in cortical activity made it possible to make this distinction as the effect of offline TMS cannot be attributed to the interruption of a signal initiating transitions.

Interestingly, similar findings have been reported for offline disruption with unilateral caloric vestibular stimulation (i.e., pouring ice-water into the ear canal) prior to viewing binocular rivalry (Miller et al., 2000). Caloric stimulation is claimed to activate contralateral hemispheric structures (Bottini et al, 1994; Vitte et al, 1996) involved in attention (Posner & Petersen, 1990) and rivalry (Lumer et al, 1998). Indeed, dominance durations were shortened when ice water was poured into the right ear (this was interpreted as activating the left hemisphere, rather than as interfering with right hemisphere activity, which may also be the case). However, similar to the TMS results in another experiment in the same study, the effect of caloric stimulation was also confined to one eye. In contrast, the results of the present study show a similar effect for both eyes, supporting a view of right parietal involvement in rivalry as general, rather than limited to one of the rivalrous stimuli.

The previous findings of fMRI activity during the perceptual transitions of rivalry, rather than during dominance phases (Lumer et al, 1998), appear at first to be at odds with the current findings. However, the TMS and fMRI findings can be reconciled by suggesting that the fMRI activity reflects increased metabolic demands in inhibitory synapses (Heeger & Ress, 2002; Logothetis et al, 2001; Mathiesen et al, 1998) during the termination of a stable bias; alternatively, such activity may result from elevated metabolism in neurons attempting to maintain the current perceptual state, just before the other image becomes dominant. And finally, sensitive multivariate fMRI analysis techniques may yet reveal activity in parietal regions associated with specific perceptual states in binocular rivalry, as has recently been demonstrated for a bistable rotating sphere (Brouwer et al, 2006).

The present findings are in line with the results presented in the previous chapter, which showed that loading working memory leads to a shortening of dominance durations in rivalry. Rendering top-down control systems unavailable to maintain perceptual biases impairs top-down control of visual competition (Desimone and Duncan, 1995, Lavie et al, 2004). This can occur either as a result of occupying these systems in a different task or of temporarily interfering with their activity using TMS. The correspondence between working memory, top-down control and right-parietal cortex is strengthened by previous findings showing that working memory (Courtney et al, 1998) and the visual short-term memory (Todd & Marois, 2004; Vogel & Machizawa, 2004) tasks are associated with activity in a network comprising frontal and parietal regions, including the superior parietal region which received TMS stimulation in this study.

The present results imply that patients with unilateral neglect (following a right parietal lesion) might show shorter dominance durations (compared to controls) in binocular rivalry, since their lesion is in a similar location to the 'virtual lesion' induced here by TMS. However, a recent study (Bonneh, Pavlovskaya, Ring, & Soroker, 2004) reported that dominance durations in neglect patients were about four times longer than those of healthy observers and right-hemisphere control patients without neglect. But unilateral neglect is often caused by damage to other cortical regions except parietal cortex, and indeed, among the six neglect patients examined, only two had parietal lesions. Furthermore, three patients (including the two who had parietal lesions) had frontal lesions. Such lesions are known to lead to perseveration. This may imply that the lengthening in rivalry dominance durations was due to a form of perseveration – either perceptual or related to motor-responses – rather than to the parietal mechanisms targeted in this study.

Interestingly, recent studies have shown that using TMS to perturb right superior parietal cortex (Beck et al, 2006) and right dorsolateral prefrontal cortex (Turatto et al, 2004) increased error rates on a change detection task, establishing a causal role for these regions in change blindness. Change detection is assumed to require the ability to allocate attention to various elements of an image (in other words, to bias processing of visual stimuli) and to involve visual short-term memory. Such functions are also likely to be involved in binocular rivalry (Blake & Logothetis, 2002; Leopold et al, 2002). These converging lines of evidence attest to the potential general importance of superior parietal cortex in visual awareness. Neuroimaging studies employing a variety of tasks have associated parietal activity with visual awareness (Beck et al, 2001; Carmel, Lavie & Rees,

2006; Eriksson et al, 2004; Kjaer et al, 2001; Kleinschmidt et al, 1998; Lumer et al, 1998; Lumer & Rees, 1999; Portas et al, 2000; Sterzer et al, 2002). The precise causal role of parietal cortex in awareness is beginning to emerge from studies manipulating this region directly.

Chapter 7:

General Discussion

7.1 Overview of findings

The research described in this thesis establishes major determinants of the top-down control of visual awareness. It also contributes to the understanding of the role of frontal and parietal cortex in the control of awareness.

7.1.1 Perceptual load and visual awareness: Presence/absence detection

Chapters 2 and 3 demonstrate that perceptual load affects visual awareness. In Chapter 2, I found that sensitivity in a presence/absence detection task was consistently reduced under high perceptual load. In all experiments, this effect could not be attributed to a difference in response criterion under different load conditions. The reduction in sensitivity under high perceptual load did not depend on the overall level of sensitivity (Experiments 1 and 2), nor was it due to the need to coordinate attention to certain locations with inhibition of others (Experiment 3). Importantly, for the effect of perceptual load to occur it was not even necessary for the stimuli for which load was manipulated to be presented concurrently with those for which awareness was assessed (Experiments 4 and 5). While participants were processing the stimuli for which perceptual load was manipulated, their sensitivity to other stimuli was reduced. Critically, no such reduction was found for stimulus presentations occurring after such processing was over (Experiment 5), indicating that the effect was indeed due to load rather than to any change in strategy (e.g., a reduction in the priority of detection performance under high load).

7.1.2 Perceptual load and visual awareness: Temporal patterns

In Chapter 3 I generalized the effect of perceptual load on visual awareness to the temporal domain, with experiments showing that when perceptual load was manipulated for a spatial search task, the subjective percept (rather than just sensitivity to whether or not a stimulus had been presented, as in Chapter 2) associated with a temporal pattern (flicker) was altered. Under high perceptual load participants were more likely to see the same flickering stimulus as steady, fused illumination (Experiment 6). This effect could not be due to different criteria for reporting flicker under different load conditions, as demonstrated using a 2IFC paradigm (Experiment 8). Possible alternative accounts, attributing the results to an effect of perceptual load on memory, were also ruled out by collecting the response to flicker before the search response (Experiments 7 and 9).

7.1.3 Neural correlates of visual awareness: Temporal patterns

Activity in regions of frontal and parietal cortex has been found in previous neuroimaging studies of visual awareness. However, the involvement of these regions in awareness of temporal patterns, such as the luminance flicker examined in Chapter 3, had not been investigated previously. The attentional modulation of flicker awareness found in Chapter 3 suggests that neural mechanisms associated with attention should indeed be involved in awareness of flicker. Specifically, I hypothesized that fronto-parietal regions previously implicated in awareness of other types of stimuli would be involved in flicker

awareness as well. In Chapter 4 I used fMRI, adapting the general approach of investigating awareness by presenting participants with physically identical stimuli that may be perceived in more than one way (e.g., Frith et al, 1999; Rees et all 2002) to investigating temporal visual awareness. This was achieved by presenting flicker at the critical flicker fusion threshold, where the same stimulus is equally likely to be perceived as flickering or as fused. Greater activity was found in bilateral frontal and left parietal cortex when participants perceived a single, fixated LED as flickering than when they perceived it as fused. Importantly, this activity was found in similar areas to those reported in previous awareness studies, indicating that a similar network of brain regions may play a general role in mediating all forms of visual awareness.

7.1.4 Working memory load and visual awareness: Binocular rivalry

In Chapter 5 I turned to investigate whether the activity of the control mechanism postulated by load theory (Lavie 2000; 2005; Lavie at al, 2004) generalizes to awareness. I examined the effects of working memory load on the temporal dynamics of binocular rivalry, a fundamental form of competition in visual awareness. I found that under high (compared to low) working memory load, the durations of dominance periods in rivalry were reduced and those of the initial mixed phase increased, indicating that loading working memory impaired the visual system's ability to maintain a stable bias in visual awareness in the face of ongoing competition between equally-salient stimuli (Experiment 11). A computational simulation ruled out the possibility that the shortening of dominance periods was due to a sampling bias resulting from the difference in

initial mixed-phase durations. The results were also not due to a difference in response characteristics under different working memory load conditions, as ascertained by presenting physical alternations rather than rivalrous ones (Experiment 12).

7.1.5 Parietal cortex and the control of visual awareness: Binocular rivalry

The results of Chapter 5 show that high level cognitive functions are involved in top-down control of binocular rivalry, and previous neuroimaging research (Lumer et al, 1998; Lumer & Rees, 1999) has suggested a role for right parietal cortex in such control. However, the correlational nature of neuroimaging data precludes the attribution of a causal role to this region in the control of binocular rivalry. In Chapter 6 I used TMS to investigate whether right parietal cortex indeed plays such a role. The results of Experiment 13 showed that applying TMS to right parietal cortex caused a shortening of dominance durations in binocular rivalry (compared to left parietal TMS and no TMS conditions). Taken together with the results of Chapter 5, this supports the conclusion that high-level brain regions and cognitive functions serve to maintain perceptual biases in binocular rivalry.

7.2 Implications for load theory

7.2.1 Relation to previous research

Load theory predicts that increasing perceptual load for particular stimuli should attenuate the perception of other stimuli (e.g., Lavie, 1995). The theory also predicts that increasing working memory load results in reduced ability to maintain biases in the allocation of processing resources in situations of competition between salient stimuli, and should therefore lead to increased interference from ignored stimuli (Lavie 2000; 2005; Lavie et al, 2004).

Previous research has supported these predictions. Increasing perceptual load has been found to decrease behavioural interference from irrelevant distractors in flanker (Lavie, 1995; Lavie & Cox, 1997; Maylor & Lavie, 1998) and Stroop-like (Lavie et al, 2003) tasks, and to eliminate negative priming (Lavie & Fox, 2000). Neuroimaging studies have found that increasing perceptual load decreases neural activity associated with irrelevant stimuli in stimulus selective brain regions (Pessoa et al, 2002; Rees et al, 1997; Yi et al, 2004), early visual cortex (Schwartz et al, 2005) and even the LGN (O'Connor et al, 2002).

Increasing working memory load has been found to increase behavioural interference from irrelevant distractors in Stroop-like (De Fockert et al, 2001) and flanker (Lavie et al, 2004) tasks, and to increase attentional capture by salient, yet irrelevant stimuli (Lavie & De Fockert, 2005). Neural activity related to ignored face stimuli was found to increase under high (compared to low) working memory load (De Fockert et al, 2001).

However, all of the research described above has employed indirect measures of perceptual processing, such as target RTs. These measures do not reveal anything about observers' awareness of stimuli – it is both a logical possibility and an established empirical finding (e.g., Marshall & Halligan, 1988; Rees et al, 2000) that stimuli can be processed without reaching awareness. Though load theory predicts that both kinds of load should affect conscious perception, the experimental evidence described in the last few paragraphs may in fact reflect modulation of purely unconscious processing.

Two previous studies have provided promising preliminary evidence suggesting that the predictions of load theory would generalize to conscious awareness, assessed with the direct, explicit measure of participants' reported percepts. Rees et al (1997) found that the duration of the motion after effect was reduced when participants performed a high (compared to low) perceptual load task while ignoring a moving stimulus. The motion after effect is a subjective visual experience, and participants reporting it are indeed reporting their conscious awareness. However, reports regarding an after effect do not reveal whether load modulated conscious perception of the moving stimulus during performance of the task.

In a different study, Cartwright-Finch and Lavie (2006) showed that increasing perceptual load exacerbated inattentional blindness. However, effects on inattentional blindness could be accounted for in terms of rapid forgetting (e.g., 'inattentional amnesia', Wolfe, 1999) or changes in observers' criteria for reporting awareness of unexpected stimuli.

7.2.2 Theoretical impact of the new findings

The purpose of the experiments reported in Chapters 2, 3, and 5 of this thesis was therefore to assess the effects of load on conscious awareness, employing experimental paradigms that would avoid the criticisms detailed above. In Chapters 2 and 3 I used direct, explicit measures of conscious awareness to conclusively demonstrate that perceptual load affects visual awareness for detection of both presence/absence and temporal patterns.

The findings presented in Chapter 5 showed that increasing working memory load shortened dominance durations and increased the initial mixed phase of binocular rivalry, implying that working memory is required to maintain biases in visual awareness during competition from other stimuli.

These experiments therefore substantially extend the scope of load theory's predictions, showing that they apply not only to interference from task-irrelevant distractor stimuli in attentional tasks, but also to conscious awareness of visual stimuli. This corroborates the intuitive notion, described in the introduction to this thesis, that attention and awareness are intimately related. However, these results go beyond this intuition (which essentially views the concepts of attention and awareness as synonymous; see Lamme, 2003 for a critique of this conceptualization). Taken together, the results of perceptual and working memory load manipulations suggest a specific relationship between attention, executive control and awareness, in which attention serves as a gating mechanism to awareness, guided by executive control functions to select stimuli for representation in consciousness.

7.3 Biases in visual competition

The idea that visual stimuli compete for neural representation and processing resources is not new. Desimone and Duncan's (1995) biased competition model, for example, suggests that this competition takes place at many levels, in a widespread network of brain regions involved in processing visual input. A flexible bias, which can be directed at spatial locations, objects, simple visual features or conjunctions of features, can determine in a top-down manner which stimuli win the competition (Desimone & Duncan, 1995; see also Pessoa, Kastner & Ungerleider, 2003). In the next two subsections I discuss the implications of my findings for the understanding of biased competition.

7.3.1 Perceptual load and biased competition

The results of Experiments 4 and 5 in Chapter 2 widen the scope of what constitutes competition between visual stimuli, by showing that for perceptual load to modulate awareness the competing stimuli do not have to be simultaneous – they just have to appear within the same temporal window in which processing and analysis take place. Competition, therefore, does not necessitate the simultaneous presence of stimuli in the visual field. Rather, the competition can be over a limited-capacity processing resource. While this resource is occupied due to ongoing processing of certain stimuli, it becomes unavailable to process others, regardless of whether they appeared simultaneously with the stimuli being processed or not.

In addition, the results of Chapter 3 show that competition can occur between stimuli that require completely different types of processing. Despite previous suggestions that spatial and temporal aspects of stimuli are processed independently (Lehky, 1985; Wilson, 1980), manipulating perceptual load for stimuli that had to be found in one of several spatial locations and analyzed in terms of shape (letters) interfered with the analysis of a fixated stimulus that had to be analyzed in terms of its temporal pattern (flicker). The strong modulation of flicker awareness, observed when load in a letter search was manipulated, suggests that the competition can be for the top-down function that selects certain stimuli for further analysis, rather than the for the analysis of specific stimulus attributes.

7.3.2 Working memory, parietal cortex and biased competition

The biased competition model (Desimone & Duncan, 1995) also suggests that top-down selection templates are stored in working memory as short-term descriptions of currently-relevant information, so that inputs matching the description are favoured for further processing. This is consistent with the increased interference from irrelevant stimuli found under high working memory load in various response-competition tasks (De Fockert et al, 2001; Lavie et al, 2004). However, it does not explain the absence of an effect of working memory load in visual search (Logan, 1978; Woodman et al, 2001), and the contrast between the finding that neural activity related to ignored stimuli in a Stroop-like task was modulated by working memory load (De Fockert et al, 2001), whereas

activity associated with irrelevant (but not response-competitive) stimuli was not (Yi et al, 2004).

Load theory (e.g., Lavie, 2000; 2005) addresses this issue by proposing that in addition to maintenance of a target template, working memory serves as an executive control function, biasing perception in situations where there is conflict between stimuli (rather than simply many stimuli in the visual field). In Chapter 5, I found that loading working memory impairs the visual system's ability to maintain a stable bias in binocular rivalry. This indicates that working memory indeed serves to maintain biases in situations where the visual system must choose between stimuli, even if there is no specific, behaviourally-relevant target template towards which priorities must be biased.

Furthermore, in Chapter 6 I found that applying TMS to right parietal cortex – a region previously implicated in both working memory (Courtney et al, 1998; Todd & Marois, 2004; Vogel & Machizawa, 2004) and binocular rivalry transitions (Lumer et al, 1998; Lumer & Rees, 1999) – also impaired the maintenance of biases in rivalry. Of course, it cannot be concluded that the neural site affected by TMS performs the function that was affected by the working memory manipulation, but the convergent results from different methodologies do support a role for high-level mechanisms, both cognitive and neural, in the control and maintenance of perceptual biases.

7.4 Attention and visual awareness

7.4.1 Neural mechanisms of temporal attention

The precise nature of the neural mechanism mediating the effect of perceptual load on flicker awareness, found in Chapter 3, requires further elucidation. Previous studies (Yeshurun & Levy, 2003; Yeshurun, 2004) have proposed, on the basis of finding a deterioration of temporal resolution at cued locations, that attention increases parvocellular activity at cued locations in retinotopic cortex, which in turn inhibits magnocellular activity at these locations. As parvocellular neurons have smaller receptive fields than magnocellular ones, this leads to better spatial resolution. However, as parvocellular neurons also have longer response latencies than magnocellular ones, the improved spatial resolution comes at the expense of temporal resolution.

This is a compelling argument, but it clearly cannot account for the results obtained in Chapter 3. Higher perceptual load in the letter search would imply more attention being deployed to the periphery (at the expense of fixation, where the flickering LED was located). This should have led to less inhibition of magnocellular neurons at fixation, and therefore to improved temporal resolution, rather than to the impairment in flicker detection that was found. It could be suggested that cuing a location changes the ratio of parvocellular to magnocellular activity, but directing attention away from a particular location does not change the ratio at that location. However, this would still lead to the

prediction that flicker detection should not be altered by perceptual load in a different location, rather than account for the impairment found here.

It is therefore likely that the neural mechanisms underlying the effect of perceptual load are different to those underlying the effects of spatial cuing. The previously-used spatial cuing paradigm (Yeshurun & Levy, 2003; Yeshurun, 2004) assessed the effects of transient attention, which is drawn involuntarily in an exogenous bottom-up manner, peaks around 120 ms after cue onset and subsides around 250 ms from cue onset. The effects of perceptual load, on the other hand, are clearly not mediated by such a mechanism, but rather by an endogenous control process with longer lasting effects (as shown in Experiment 4 and 5 of Chapter 2). They are therefore likely to be manifested neurally in an as yet unknown, entirely different way.

7.4.2 Attention to the temporal characteristics of a stimulus

The results of Chapter 3 demonstrated that an attentional manipulation can alter awareness of a temporal pattern. In Chapter 4, brain activity correlated with flicker detection was found in a network of frontal and parietal regions previously associated with awareness, but also with attention (Naghavi & Nyberg, 2005; Wojciulik & Kanwisher, 1999). Though in many previous neuroimaging studies of visual awareness, findings of activity in this network could be attributed to shifts in spatial attention (e.g., Beck et al, 2001; 2006; Dehaene et al, 2001; Kjaer et al, 2001; Sterzer et al, 2002), in Chapter 4 the use of only a single, fixated LED with a very small spatial extent effectively rules out this possibility.

An account involving attention is still plausible, but would suggest that attention can be specifically directed at the temporal, rather than the spatial, characteristics of a stimulus. Furthermore, the substantial overlap between the network of brain regions activated in this study and the areas activated in previous studies suggests that a common, highly flexible function, distributed throughout frontal and parietal cortex, is involved in directing attention to either spatial or temporal stimulus characteristics.

Though the fronto-parietal activity associated with awareness of flicker could reflect the deployment of attention to the flickering stimulus, this cannot be asserted with certainty as attention was not directly manipulated in this study. Therefore, even if this activity is attention-related, it remains unclear in what specific way. Random fluctuations in attention, positively correlated with fronto-parietal activity, could have led to better flicker detection. Alternatively, the rapid onsets of flicker, on trials in which it was perceived, could have drawn attention and led to increased activation in the fronto-parietal network.

7.4.3 Parietal activity and visual awareness

In Chapter 4, fMRI activation associated with flicker awareness was found in both frontal and parietal cortex. This is in line with findings from previous imaging studies of visual awareness (Naghavi & Nyberg, 2005; Rees et al, 2002), and corroborates the view that for conscious experience to arise, activity in the dorsal stream, as well as the ventral stream, is required (e.g., Driver & Mattingley, 1998; c.f. Milner & Goodale, 1995).

But whereas the frontal activation associated with flicker awareness was bilateral, parietal activation was lateralized to the left. In contrast, previous neuroimaging findings (Lumer et al, 1998; Lumer & Rees, 1999) as well as the TMS study in Chapter 6 of this thesis have implicated right parietal cortex in a different awareness-related phenomenon, binocular rivalry. Furthermore, in most neuroimaging studies of visual awareness to date, parietal activation has been bilateral; where it was not, it was right-lateralized (see Naghavi & Nyberg, 2005 for a review).

The finding of left-lateralized parietal activation related to temporal awareness is therefore novel, and requires explanation. One possibility concerns the specifically temporal nature of the flicker stimulus used in Chapter 4. A study comparing attention to spatial locations with attention to time intervals (Coull & Nobre, 1998) established that while there was an overlap between neural systems involved in both kinds of attention, there were also hemispheric asymmetries, with right parietal cortex showing more activation during spatial attention, and left parietal cortex showing more activation during temporal attention. The task used in that study (involving orienting of attention towards particular time intervals in anticipation of target presentation) was very different from the experimental paradigm used here, and the temporal intervals used were much longer (300-1500 ms) than those whose detection is required for flicker perception. However, the present results support a theoretical framework within which the left hemisphere is specialized for temporal processing and analysis of serial (rather than spatial) information (e.g., Merzenich et al, 1996). Further research is required to assess the veracity of this distinction.

7.5 Future research

7.5.1 Load and unconscious perceptual processing

The research presented in this thesis establishes the effect of perceptual load – in other words, of an attentional manipulation – on the degree to which a stimulus is consciously perceived. Though this indicates that the availability of attentional resources is a necessary condition for conscious perception, the relationship between perception, attention and awareness is likely to be more complex. There is evidence that perception can occur in the absence of awareness (for a review, see Merikle, Smilek & Eastwood, 2001), and attention can be oriented toward stimuli without awareness both in normal observers (e.g., McCormick, 1997) and in patients with blindsight (e.g., Kentridge, Heywood & Weiskrantz, 1999).

This raises the question of whether there is a qualitative difference between consciously and unconsciously perceived stimuli. For example, does perceptual load determine the degree of perceptual processing that unconscious stimuli receive? By definition, investigating this possibility would have to rely on indirect measures of processing, such as effects of perceptual load on RTs or on after effects. For example, would after effects associated with oriented gratings suppressed from awareness (e.g., by continuous flash suppression, where monocularly-presented stimuli are masked by a dynamic pattern presented to the other eye; Tsuchiya & Koch, 2005) be modulated by perceptual load? If such modulation does indeed occur, this would imply that attention may control gating to awareness, but operates on levels of processing that precede it.

7.5.2 Further effects of working memory load in visual awareness

Increasing working memory load leads to greater interference from irrelevant distractors (e.g., Lavie et al, 2004), and in Chapter 5 of this thesis I showed that it impairs maintenance of biases in binocular rivalry. This result implies that working memory may serve a general role in visual awareness – that of controlling stimulus processing prioritization. However, in order to make this general claim about the role of working memory in awareness it is necessary to demonstrate similar effects in other paradigms assessing visual awareness. For example, the effect of working memory load in paradigms such as those used in Chapter 2 (presence/absence detection) and 3 (flicker awareness) could be investigates. Note, however, that as described in **Section 7.3.2**, working memory is only likely to have such effects if the stimuli used directly conflict with each other, as was the case for the binocular rivalry stimulus in Chapter 5.

An interesting possibility regards inattentional blindness. If loading working memory leads to poorer control over the selection of stimuli for processing, this leads to the counter-intuitive prediction that high working memory load should increase awareness of the unexpected task-irrelevant stimulus, reducing levels of inattentional blindness. Though inattentional blindness suffers from various limitations as an experimental paradigm (see **Section 1.4.2**), such an effect would still be a striking demonstration of the role of working memory in visual awareness. Furthermore, the result predicted by load theory would weaken the 'inattentional amnesia' account of inattentional blindness (Wolfe, 1999). If inattentional blindness is indeed due to forgetting of the critical stimulus, then

loading working memory should increase inattentional blindness (rather than decrease it, as predicted by load theory).

7.6 Conclusions

In this thesis I established the critical role of different types of load in determining visual awareness. I used direct, explicit measures of awareness to show that increasing perceptual load for certain stimuli impairs conscious awareness of other stimuli, both shapes and temporal patterns, even when these are fully expected and serve as targets. I found that presentation of these targets does not have to be simultaneous with those that perceptual load is manipulated for – it is sufficient that they need to be processed within the same time window. I also investigated the neural correlates of awareness of temporal patterns, finding that a fronto-parietal network previously associated with awareness is involved in this under-researched form of visual experience. I investigated the effects of working memory load on visual competition in awareness, by observing its effect on binocular rivalry, and found that increasing such load impaired the visual system's ability to maintain a stable, top-down bias. Finally, I used TMS to establish a causal role for right parietal cortex in the maintenance of top-down bias in rivalry. Taken together, my findings extend the scope of Lavie's load theory to visual awareness, and confirm the involvement of high-level brain regions in the top-down control of awareness.

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